Offshore Characteristics in the Deep Waters of the Strait of Georgia as Indicated by Bathypelagic Fish[1]

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ABSTRACT

An attempt is made from oceanographical observations to explain the occurrence of certain bathypelagic species of fish which have been captured in the bottom waters of the southern Strait of Georgia. It is noted that there is a considerable seaward surface flow of water from the Fraser River. The water from intermediate depths over the continental shelf forms the inflowing deep water of Juan de Fuca Strait mixing with the Fraser River water in the turbulent channels of the San Juan Archipelago. This mixture forms the deep inflowing water of southern Strait of Georgia and the outflowing surface water of the Juan de Fuca Strait as shown by salinity distribution and current measurements. The net inward movement of deep water is suggested as an agent of transport or a directive factor for the occurrence of these fish in this region. Physical and chemical conditions of the deep water in the Strait of Georgia are shown to be only slightly different from those found in the intermediate offshore water. It is probable that a combination of factors provides conditions suitable for survival of these species in the deep water of the southern Strait of Georgia.

INTRODUCTION

Attention has been drawn recently to the capture of at least four species of fish which are quite foreign to inshore coastal waters of British Columbia. The possible application of these fish as biological indicators of a particular mass of offshore oceanic water in the Strait of Georgia is considered.

Biologists have long marvelled at the diversity of the flora and fauna in the Strait of Georgia. It has already been pointed out (Cameron and Mounce, 1922) that, "species are found within the limits of the strait which extend northwards to the Arctic, but no further south, and other species which extend at least to the waters of Southern California, but no further north". It was agreed even then that this diversity in species is probably due to the diversity of conditions which exist in the strait waters.

ACKNOWLEDGMENTS

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OCCURRENCE OF FOREIGN FISH

Two species of hatchet-fish, both recorded for the first time in British Columbia, were taken in the Strait of Georgia. One species (*Argyropelecus*

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olfersi) was caught by a shrimp trawl on June 13, 1953, in English Bay at a depth of 55 meters (Area I, Fig. 1). A representative of the other species (*Argyropelecus sladeni*) was taken by a shrimp trawler off the mouth of the Fraser River at a depth of 75 meters on March 14, 1953 (Barraclough, MS). Both these species are found at depths ranging from 274 to 4,000 meters in the Pacific, Atlantic, Indian, and Antarctic Oceans (Clemens and Wilby, 1949).

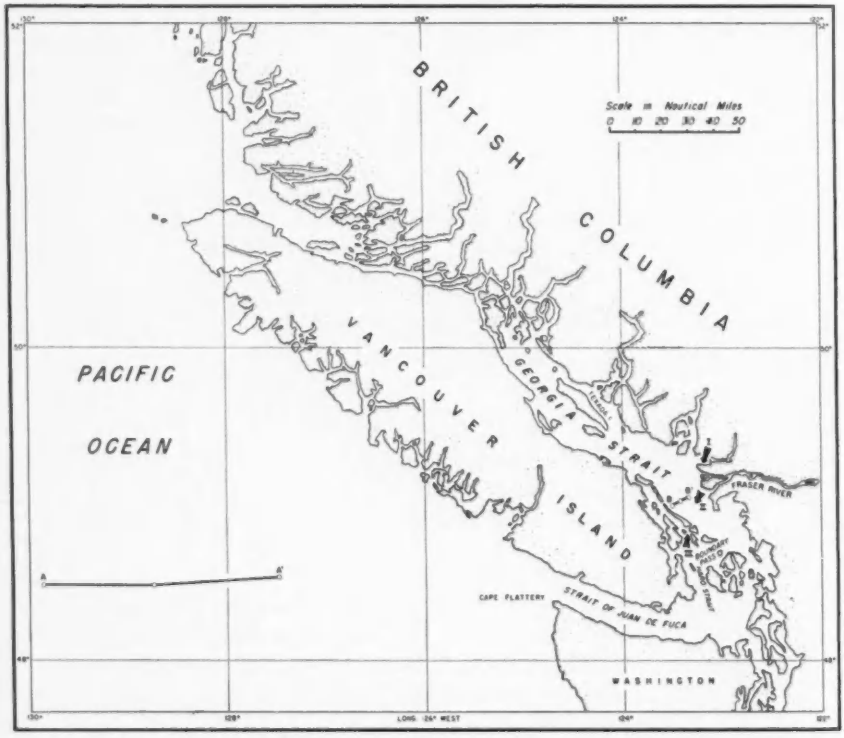

FIGURE 1. Chart of coastal British Columbia showing regions I, II and III where foreign fish were captured in the Strait of Georgia.

The first inshore record of a viper fish (*Chauliodus macouni*) was that of an individual taken in a shrimp trawl off the mouth of the Fraser River during April, 1947, at a depth of 73 meters (Barraclough, 1950). A second specimen was caught by a trawler fishing at a depth of from 105 to 110 meters near Canoe Pass buoy off the mouth of the Fraser River (Area II in Fig. 1) on March 4, 1951 (Barraclough, MS). The only other records of occurrence for this species off the British Columbia Coast consist of the large numbers taken by the International Fisheries Commission in tow nets at depths ranging from 100 to 890 meters off the west coast of Vancouver and Queen Charlotte Islands (Chapman, 1940).

A deep-sea species of liparid (*Careproctus melanurus*) was caught on

January 7, 1953, in a trawl net at a depth of 91 meters in Swanson Channel near the southern end of the Strait of Georgia (Area III in Fig. 1) (Barraclough, MS). This species has been reported previously from British Columbia to southern California, at depths from 519 to 1602 meters.

It is noted that all these bathypelagic species have been found off the Fraser River estuary or at the southern end of the Strait of Georgia. All have been taken by small-meshed trawls. It is true that more trawling of this kind is done in this vicinity than elsewhere in the strait, but, since no specimens have turned up in any other part of the strait, it appears that these species occur principally, even if not entirely, in the southern area.

DIRECTIVE FACTORS

Consideration must be given, first of all, to the means of entry of these fish into the deep waters of the Strait of Georgia if they are not native to this region. Currents may be the agent of transport for these species, particularly since they are weak swimmers. Although currents in the strait are predominantly tidal, there is also a net flow resulting from the freshwater runoff. As the Fraser River discharges into the Strait of Georgia its water forms a layer of brackish water on the surface of the denser sea water, mixing as it advances seaward (Tully, 1952). Thus salt water is constantly being swept out to sea near the surface. To replace this salt water there must be a net inflow of sea water at depth, otherwise the basin would become gradually filled with fresh water. Deep currents measured in Juan de Fuca Strait have been shown to reach an average maximum of

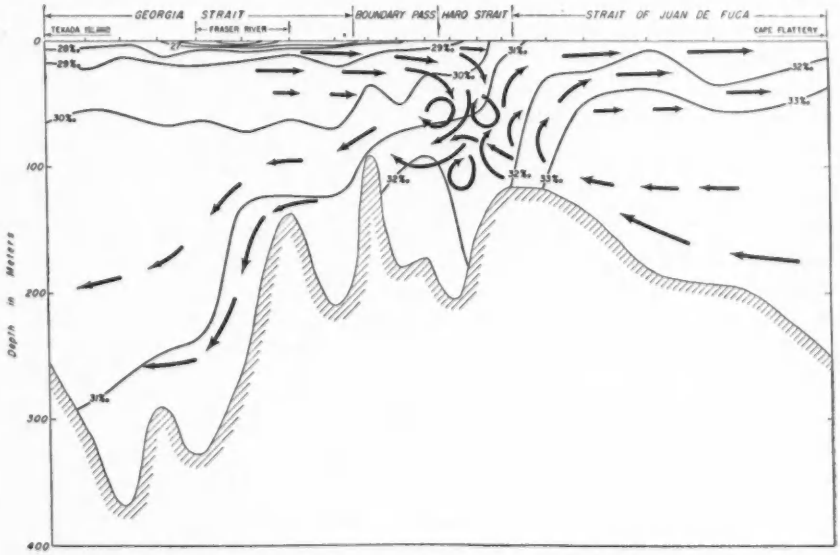

FIGURE 2. Vertical distributions of salinity and current directions in the Strait of Georgia–Juan de Fuca Strait system. Data from synoptic surveys, September, 1952.

0.77 m./sec. (1.5 knots) on the flood as compared with 0.51 m./sec. (1.0 knots) on the ebb (Herlinveaux, 1953), or a net inflow of 0.26 m./sec. (0.5 knots). In addition, the duration of flow on the flood is greater than that on the ebb in the deep water. Consequently, the deep water undergoes a net movement inward as well as the tidal movement back and forth.

The vertical distribution of salinity from Texada Island in the Strait of Georgia to the outer end of Juan de Fuca Strait is shown in Figure 2. The high vertical stratification off the Fraser River is shown by the large salinity change in the upper 20 meters. The relatively homogeneous water mass in the inter-island channels to the south results from the intensive tidal mixing in that area. In Juan de Fuca Strait a slight vertical stratification again appears. The diagram shows how the mixed water in the channels of the San Juan Archipelago forms the deep water in the Strait of Georgia and the surface water in Juan de Fuca Strait, as represented by the layer between 31 and 32‰. The net circulation as inferred from the salinity distribution and current measurements is shown by the arrows.

OCEANOGRAPHICAL CONDITIONS

From casual observation one might conclude that, of all the areas in the Strait of Georgia, the one most unlike any offshore region is that area most

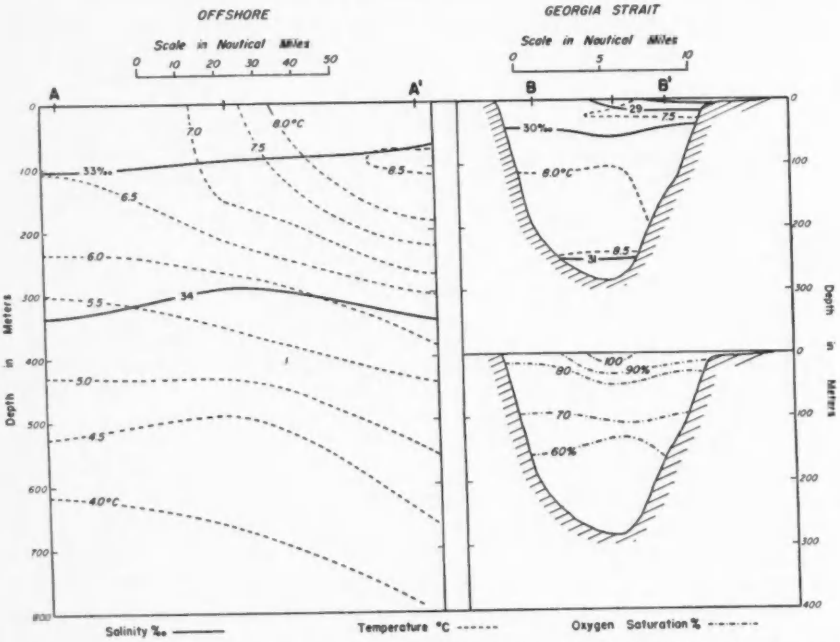

FIGURE 3. Sections showing water properties offshore and in the Strait of Georgia. Positions are shown in Figure 1. Data from surveys—A A', March, 1952; B—B', March, 1953.

influenced by the Fraser River. Studies have shown this to be true for the surface water (Hutchinson and Lucas, 1931). But when consideration is given to certain physical and chemical properties of the bottom water, conditions are found comparable to the intermediate offshore waters (Fig. 3).

SALINITY. The vertical distribution of salinity across the Strait of Georgia shows that the fresh water is confined mainly to the upper 10 meters in its dilution effect (Waldichuk, 1952). A very sharp boundary exists between the brackish water at the surface and the deeper saline water. Seasonal changes in salinity of this deep water are small and the year round salinity is less by only about 2‰ than that of the intermediate water off the west coast of Vancouver Island (see Fig. 3).

TEMPERATURE. The temperature at depth has been shown also to vary little from summer to winter and generally maintains itself between 7.5° and 8.5°C. (Waldichuk, 1953). This temperature range is very similar to the temperatures occurring at depths from 100 to 200 meters in waters off the west coast of Vancouver Island (Fig. 3).

OXYGEN. Dissolved oxygen concentration in the Strait of Georgia are relatively high at all depths and during all seasons (Waldichuk, 1953). Oxygen content near the bottom seldom drops below 50% of saturation. The trend of isopleths of oxygen corresponds closely to that of the isohalines shown in Figure 2. In the Strait of Georgia there is high stratification near the surface with some supersaturation. Tidal action in the channels to the south mixes the water to homogeneity by bringing deep water containing less oxygen to the surface. In Juan de Fuca Strait there is a slight vertical stratification in oxygen concentration again. Because the gradient of dissolved oxygen is never very large except near the surface, oxygen cannot be considered a directing or limiting factor (Fry, 1947).

LIGHT. An important factor to consider in so far as the deep sea forms are concerned is the light condition under which they live. Animals living in the abyssal depths of the ocean have often become adapted to the absence of sunlight by the development of extremely large, sensitive eyes, particularly suited to detecting the weak luminescence produced by their own or other species. Great depths are not found in the Strait of Georgia, but conditions of poor lighting are duplicated by the presence of large quantities of silt in the upper layers which reduce very markedly the transmission of light. Thus the twilight conditions of the open ocean at 200 meters can be duplicated at depths of only 20 meters in regions of the Strait of Georgia influenced most by the silt of the Fraser River.

SUMMARY

It is probable that the presence of bathypelagic species in the southern part of the Strait of Georgia can be accounted for by the movement of intermediate offshore water into the deep water of the strait. Because of the combination of the physical and chemical factors present there, conditions are produced that are similar to those found in the normal habitat of these species.

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Polychaetous Annelids of Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound[1]

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ABSTRACT

A collection of 74 species of polychaetous annelids, the greater part of which was obtained by the *Calanus* expeditions of 1947–1952 in Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound, is described. Twelve species are new records for the Canadian eastern arctic, and 2 are new for North America. The zoogeographical relationships of the known Canadian eastern arctic polychaete fauna are discussed.

INTRODUCTION

This paper deals principally with the polychaetes collected by the *Calanus* expeditions from 1947 to 1952, in Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound, in the Canadian eastern arctic. The material has been supplemented by a collection made during the summer of 1953 in Frobisher Bay, Cumberland Sound, Padloping Island and intermediate waters, made available to the author by the collector, D. V. Ellis. Also a list of 9 species, collected in Hudson Strait and Cumberland Sound and at Somerset Island, and identified by E. and C. Berkeley, has been provided by them for inclusion here.

The material includes some 1,800 specimens of polychaetes of 74 species, representing 27 families. None of the species is new, but 12 species are new records for the Canadian eastern arctic, and 2 species apparently have not been recorded formerly from North America. The specimens were collected chiefly by dredging, trawling and intertidal collecting, and additional forms were acquired from the stomachs of fishes and seals. The depth range of the collections is from the intertidal area to 274 metres.

During recent years reviews of the known polychaete faunas of various northern regions have appeared, including West Greenland (Wesenberg-Lund, 1950) and Alaska (Hartman, 1948), areas immediately adjacent to the Canadian north. The polychaetes of southeastern Canadian waters have been treated (Treadwell, 1948), but the records here are incomplete for the region north of the Strait of Belle Isle. For the great region extending from southern Labrador west to Alaska, however, no compilation of polychaete records has been published. Examination of the literature shows that at least 139 species of polychaetes are now known from this area, and that at least 134 of these species are recorded from the eastern part of the area, from Labrador west to and including Hudson Bay.

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In the following systematic account of the species, the collections are described giving station numbers and the numbers of specimens taken at each. For locations and depths of the *Calanus* stations reference may be made to the two station lists of the *Calanus* expeditions (Dunbar and Grainger, 1952; Grainger, 1954). The station list of the Ellis collections is given in Table I. The Berkeley

TABLE I. Station list of the Ellis collections.

Station	Date	Depth	Location
Frobisher Bay			
A6	19–21/6/53	intertidal	Becher Peninsula, 63° 24′ N., 67° 49′ W.
A6 dredge	"	not more than 4 m.	as above
A7	22/6/53	intertidal	island west of Culbertson Island, 63° 23′ N., 67° 59′ W.
A8	26/6–1/7/53	intertidal	Becher Peninsula, 63° 27′ N., 67° 51′ W.
A8h	"	not more than 4 m.	as above
A9	1–4/7/53	intertidal	Becher Peninsula, 63° 33′ N., 67° 59′ W.
A9f	"	not more than 4 m.	as above
A12	4/7/53	intertidal	inlet west of Burton Bay, 63° 38′ N., 68° 17′ W.
A12c	"	not more than 4 m.	as above
A14	6–24/7/53	intertidal	Koojesse Inlet, 63° 40′ N., 68° 28′ W.
A15	13/7/53	intertidal	Jordan River, 63° 46′ N., 68° 59′ W.
A17	25/7/53	intertidal	Chase Island, 63° 05′ N., 66° 55′ W.
A20	26/7/53	intertidal	bay east of Cape Carter, Loksland, 62° 25′ N., 64° 54′ W.
A20a	"	floating *Laminaria*	as above
A23	27/7/53	intertidal	near Cape Chapel, Loksland, 62° 25′ N., 64° 56′ W.
Between Frobisher Bay and Cumberland Sound			
A26	28/7/53	floating *Laminaria*	west of Cape Farrington, 62° 51′ N., 64° 49′ W.
A26b	"	intertidal	as above
A27	29/7–2/8/53	intertidal	Siniyah Harbour, 62° 54′ N., 64° 40′ W.
Cumberland Sound			
A32	4–13/8/53	intertidal	Pangnirtung, 66° 09′ N., 65° 45′ W.
A43	11/8/53	intertidal	mouth of Pangnirtung Fjord, 66° 04′ N., 65° 56′ W.
Davis Strait			
A44	14–26/8/53	intertidal	Padloping Island, 67° 03′ N., 62° 44′ W.
A44c	"	not more than 4 m.	as above

material, including 9 species collected by H. M. Rogers on the Eastern Arctic Patrol of 1937, at Fort Ross (Somerset Island), Lake Harbour (Hudson Strait) and Pangnirtung (Cumberland Sound), published for the first time here, is referred to under Canadian arctic distribution. In the distributional records of the species recorded by Berkeley and Berkeley (1943) additional data, provided by the Berkeleys and not included in the original publication, are given here.

Distribution records under "Canadian arctic" refer to the region from southern Labrador to Alaska. In distributional accounts under "further distribution", the terms "arctic", "subarctic" and "boreal" are used as defined by Dunbar (1953).

The following species apparently are recorded here for the first time from North American waters: *Autolytus prolifer* (Müller) and *Lysilla lovéni* Malmgren.

The following species are new records for the eastern Canadian arctic: *Eulalia bilineata* Johnston, *Eteone flava* (Fabricius), *Tomopteris planktonis* Apstein, *Autolyus prolifer* (Miller), *Autolytus verrilli* Marenzeller, *Haploscoloplos elongata* (Johnson) (identified by the Berkeleys), *Lysippe labiata* Malmgren, *Amphitrite groenlandica* Malmgren, *Amphitrite affinis* Malmgren, *Laphania boecki* Malmgren, *Lysilla lovéni* Malmgren and *Potamilla neglecta* (Sars).

Polynoidae

Gattyana cirrosa (Pallas)

Fauvel, 1923, p. 49, fig. 17.

Canadian arctic: Sabine (1824), Melville Island (*Polynoe scabra*); McIntosh (1879), Ellesmere Island (*Nychia cirrosa*); Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Bernard Harbour, Dolphin and Union Strait (*G. cirrhosa*); Treadwell (1937), Foxe Basin, Melville Peninsula, Cobourg Island; Berkeley and Berkeley (1943), Wakeham Bay.

Further distribution: Circumpolar, in arctic, subarctic and more southern waters.

Collections: 102 (1), 203 (2), Ogac Lake (7).

Gattyana amondseni (Malmgren)

Malmgren, 1867, p. 5, pl. I, fig. 4.

Canadian arctic: Moore (1909), Labrador.

Further distribution: Chiefly in subarctic and more southern areas of the Atlantic, but recorded as far west as Alaska (Hartman, 1948).

Collection: 416 (1). This single specimen, a mud-encrusted individual about 28 mm. long, was taken from a depth of 274 m. in relatively warm Clearwater Fjord, Cumberland Sound.

Eunoe nodosa (Sars)

Fauvel, 1923, p. 51, fig. 18.

Canadian arctic: McIntosh (1879), Ellesmere Island (*E. oerstedi*); Ditlevsen (1909), Ellesmere Island (*Harmothoe nodosa*); Ditlevsen (1937), Jones Sound (*Harmothoe nodosa*); Treadwell (1937), northern Labrador, Foxe Basin, Melville Peninsula, Cobourg Island; Berkeley and Berkeley (1943), Hudson Bay.

Further distribution: Circumpolar, in arctic, subarctic and more southern regions.

Collections: 33 (1), 45 (1, from the stomach of *Gadus callarias*), 102 (2), 103 (1), 106 (1), 126 (2), 201C (3), 208 (3), 210 (1), 226 (1), 231 (6), 319 (2), 322 (1), 333 (1).

Harmothoe imbricata (L.)

Fauvel, 1923, p. 55, fig. 18.

Canadian arctic: Sabine (1824), Melville Island (*Polynoe cirrata*); Packard (1863), Labrador (*Lepidonotus cirrata*); Packard (1867), Labrador; McIntosh (1879), Ellesmere Island; Verrill (1879), Cumberland Sound; Whiteaves (1885), Burwell; Fewkes (1888), Ellesmere Island; Ditlevsen (1909), Devon Island, Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Burwell, Hudson Bay, Bernard Harbour, Dolphin and Union Strait;

Treadwell (1937), Labrador, Foxe Channel, Foxe Basin, Melville Peninsula, Cobourg Island; Berkeley and Berkeley (1943), Wakeham Bay, Hudson Bay; Berkeley and Berkeley (1944), Bernard Harbour, Dolphin and Union Strait, Coronation Gulf; the Berkeleys (pers. comm.), Lake Harbour.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern regions.

COLLECTIONS: 1A (1), 12 (1), 33 (1), 40 (19), 51 (4), 58 (5), 64 (18), 102 (1), 203 (8), 210 (2), 226 (2), 234 (1), 310 (4), 317 (2), 318 (1), 319 (5), 402 (21), 404 (2), 406 (2), 412 (2), A6 dredge (2), A6 (2), A7 (2), A8 (10), A9 (6), A9f (1), A12c (2), A15 (2), A17 (2), A20 (4), A20a (1), A23 (8), A26 (9), A26b (3), A44c (12).

Lagisca rarispina (Sars)

Fauvel, 1923, p. 76, fig. 28 (*L. extenuata*).

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*Harmothoe rarispina*); Ditlevsen (1909), Ellesmere Island (*Harmothoe rarispina*); Chamberlin (1920), Burwell; Ditlevsen (1937), Exeter Sound (*Harmothoe rarispina*); Berkeley and Berkeley (1943), Hudson Bay; Vibe (1950), Ellesmere Island (*L. extenuata*).

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 13 (1); 18 (11), 20 and 21 (1), 30 (3), 58 (3), 69 (1), 102 (2), 103 (9), 106 (1), 107 (1), 203 (1), 206 (1), 208 (5), 210 (7), 225 (1), 226 (13), 231 (2), 319 (2), 322 (3), 331 (2), 333 (1), 402 (1), 404 (1), 406 (3), 418 (2), Ogac Lake (2), A7 (3).

SIGALIONIDAE

Pholoe minuta (Fabricius)

Fauvel, 1923, p. 120, fig. 44.

CANADIAN ARCTIC: Packard (1867), Labrador; Ditlevsen (1909), Ellesmere Island; Chamberlin (1920), Bernard Harbour.

FURTHER DISTRIBUTION: Possibly circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 102 (1), 217 (2), Ogac Lake (18).

PHYLLODOCIDAE

Phyllodoce groenlandica Oersted

Fauvel, 1923, p. 153, fig. 54.

CANADIAN ARCTIC: Packard (1867), Labrador; McIntosh (1879), Ellesmere Island; Verrill (1879), Cumberland Sound; Chamberlin (1920), Bernard Harbour, Melville Island (*Anaitides groenlandica*); Treadwell (1937), Fury and Hecla Strait; Berkeley and Berkeley (1943), Wakeham Bay, Hudson Strait, Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern regions.

COLLECTIONS: 11 (1), Burwell (3, from stomachs of *Gadus callarias*), 102 (4), 107 (1), 203 (1), 229 (1), A9 (1), A12 (1).

Eulalia bilineata Johnston

Fauvel, 1923, p. 162, fig. 58.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: New England (Hartman, 1942), western Canada (Berkeley and Berkeley, 1948), Jan Mayen, Spitzbergen and northern Europe (Wesenberg-Lund, 1953), North Sea to the Mediterranean (Fauvel, 1923).

COLLECTION: 103 (1).

Eteone longa (Fabricius)

Fauvel, 1923, p. 172, fig. 62.

CANADIAN ARCTIC: Packard (1867), Labrador (*E. cylindrica*); Ditlevsen (1909), Ellesmere Island (*E. cylindrica*); Chamberlin (1920), Bernard Harbour; Berkeley and Berkeley (1943), Burwell, Wakeham Bay; the Berkeleys (pers. comm.), Cumberland Sound.

FURTHER DISTRIBUTION: Probably circumpolar, predominantly in arctic and subarctic areas, also in more southern regions.

COLLECTIONS: 1 (1), 38 (2), 44 (1), 51 (2), 101 (2), Burwell (2, from stomachs of *Gadus callarias*), 107 (1), 216 (3), 222 (1), 229 (1), 310 (1), 319 (1), 402 (1), 413 (3), A8h (2), A8 (6), A9 (2), A12 (4), A14 (4), A20 (5).

Eteone flava (Fabricius)

Fauvel, 1923, p. 173, fig. 62.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: Possibly circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: A8 (2), A9 (1), A26 (1).

TOMOPTERIDAE

Tomopteris planktonis Apstein

Apstein, 1900, p. 42, pl. XI, figs. 22–23.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: This species is distributed widely in the middle part of the North Atlantic, most frequently over great depths (Wesenberg-Lund, 1950), also in the South Atlantic and Indian Oceans (Fauvel, 1923). It was taken off southeastern Canada at the outer stations of the Canadian Fisheries Expedition of 1914–15 (Huntsman, 1921). The most northern collection originated in Qarajags Isfjord, 70° N., West Greenland, where one specimen only was taken (Wesenberg-Lund, 1950).

COLLECTION: 103 (2).

With the exception of the length of the second cirri, which are about two thirds the length of the body in these specimens, excellent agreement exists between them and Apstein's (1900) description. The presence of these specimens in the northeastern corner of Ungava Bay points to an Atlantic influence in this area.

HESIONIDAE

Castalia aphroditoides (Fabricius)

McIntosh, 1908, p. 125, pl. LVIII, fig. 18 (*C. arctica*).

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island, Devon Island (*C. fabricii*); Ditlevsen (1937), Ellesmere Island (*C. fabricii*); Berkeley and Berkeley (1943), Wakeham Bay (*C. fabricii*). Chamberlin (1920) recorded *Psammate aphroditoides* (= *C. aphroditoides*) from Bernard Harbour and Alaska, stating, however, that it was not the same as McIntosh's (1908) *C. arctica*, which according to Chamberlin was not a synonym of *C. aphroditoides* at all but referable to another species. Wesenberg-Lund (1953), however, synonymizes the *C. arctica* of McIntosh with *C. aphroditoides* of East and West Greenland.

FURTHER DISTRIBUTION: This species is found chiefly to the north of the Atlantic area, possibly as far west as the Bering Sea, and appears to be limited principally to the arctic and subarctic regions.

COLLECTIONS: Ogac Lake (5), 402 (3), A6 dredge (1), A9 (1), A26 (1).

Syllidae

Syllis cornuta Rathke

Wesenberg-Lund, 1947, p. 6, fig. 1.

Canadian arctic: Fewkes (1888), Ellesmere Island (*Chaetosyllis oerstedi*); Ditlevsen (1909), Ellesmere Island (*S. fabricii*).

Further distribution: Possibly circumpolar, in arctic, subarctic and more southern waters.

Collection: 3 (1, planktonic).

Syllis fasciata Malmgren

Malmgren, 1867, p. 43, pl. VII, fig. 47, pl. VIII, fig. 52.

Canadian arctic: Ditlevsen (1909), Ellesmere Island.

Further distribution: Possibly circumpolar, predominantly arctic and subarctic.

Collections: 317 (1), 319 (3), 322 (1), 334 (1), 406 (1). These specimens, all atokous, were collected only in Frobisher Bay.

Eusyllis blomstrandi Malmgren

Wesenberg-Lund, 1947, p. 11, fig. 3.

Canadian arctic: Ditlevsen (1909), Ellesmere Island (*S. monilicornis*).

Further distribution: An arctic, subarctic and more southern form, this species is recorded from eastern Spitzbergen (Augener, 1928), Franz-Joseph Land (Annenkova, 1932), Novaya Zemlya, Kara Sea, Iceland, West Greenland, Scandinavia and south to the Mediterranean (Wesenberg-Lund, 1953), in the Pacific area from British Columbia (Berkeley and Berkeley, 1948) and from New England.

Collection: 226 (15). These specimens, all atokous, were taken only at the Button Islands, at the eastern end of Hudson Strait.

Autolytus prolifer (O. F. Müller)

Wesenberg-Lund, 1947, p. 19, figs. 8–9.

Canadian arctic: No previous record.

Further distribution: This is predominantly a subarctic and more southern species, recorded from West and East Greenland, Spitzbergen, Kara Sea, Scandinavia, Denmark and farther south in the Atlantic (Wesenberg-Lund, 1953), and from Franz-Joseph Land (Augener, 1913). There is apparently no record of this species from North America or from the Pacific area.

Collections: 1 (2, planktonic), 58 (1), 101 (3, planktonic), 103 (2, planktonic), 226 (2), 231 (1, planktonic).

Of these 11 specimens, 3 were atokous, 4 sacconereis and 4 polybostrichus forms. All but 2 of the atokous individuals were collected in Ungava Bay; the other 2 were taken at the Button Islands, at the eastern end of Hudson Strait.

The largest atokous specimen, 10 mm. long, had formed a bud on the stalk. This occurred on the fourteenth chaetiger, as was found by Augener (1928, p. 724) at Spitzbergen. A similar condition was found in one of the other atokous forms, an individual 9 mm. long.

In all the pelagic forms there were anteriorly 3 unmodified segments. Of these 8 specimens, 7 were collected between June 24 and July 20; one was taken on August 27. None of the 4 females bore eggs.

Autolytus prismaticus (Fabricius)

Wesenberg-Lund, 1947, p. 24, figs. 10–12.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*A. longisetosus*); Moore (1909), Labrador (*A. longisetosus*); Chamberlin (1920), Dolphin and Union Strait; Treadwell (1937), Foxe Basin (*Polybostrichus longosetosus*).

FURTHER DISTRIBUTION: From its known distribution this is apparently predominantly a subarctic species, recorded from West Greenland, East Greenland (southern part), Spitzbergen (common in the west, sparse in the east) and northwestern Iceland (Wesenberg-Lund, 1953), in the North Pacific, south to British Columbia (Berkeley and Berkeley, 1948) and on the American east coast, south to New England (Treadwell, 1948).

COLLECTIONS (all planktonic): 1 (9), 3 (14), 7 (29), 9 (54), 13 (10), 18 (2), 37 (3), 38 (1), 51 (2), 57 (1), 60 (38), 101 (13), 103 (20), 129 (1), 229 (1), 301 (3), 335 (1).

Of 202 specimens of this species, 201 were collected in Ungava Bay, and only one was taken elsewhere, in Jackman Sound, southern Frobisher Bay.

Both polybostrichus and sacconereis forms were collected, and in all there were 6 unmodified segments anteriorly. In at least some of the males, ramified dorsal cirri, similar to those shown by Wesenberg-Lund (1947, p. 30) were present, on the anterior segments of the modified portion.

In the 3 seasons during which most of the specimens were obtained, 1947, 1948 and 1949, almost all were collected before early August. In 1947, 118 individuals were taken between June 24 and the end of July, and only 6 were collected in August. In 1948, all 39 specimens were secured before August 2. In 1949, 33 individuals were taken between June 26 and July 6, and only one more was obtained on August 25.

In 1947, the first females were collected on June 24, were 2–3 mm. long, and did not appear to be carrying eggs. During early July of the same year the females were 4–5 mm. long, the bodies were curved, and within the arch, on the ventral surface, eggs were present. Individuals taken in late July and August were 7–10 mm. long, with the bodies curved and eggs carried ventrally. The maximum production of sacconereis and polybostrichus stages of this species would appear to occur during early July in Ungava Bay, and to be followed by a gradual diminishing of numbers in late July and August.

Autolytus verrilli Marenzeller

Wesenberg-Lund, 1947, p. 33, figs. 14–15.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: Principally an arctic and subarctic species, it occurs in West Greenland (Wesenberg-Lund, 1950), Iceland and Spitzbergen (Wesenberg-Lund, 1953, *A. alexandri*), Franz-Joseph Land (Annenkova, 1932), Bering Sea (Chamberlin, 1920, *A. alexandri*) and New England (Verrill, 1881, *A. alexandri*). Wesenberg-Lund (1950) refers to this species as being one of the most northerly distributed of the polychaetes.

COLLECTIONS (all planktonic): 1 (3), 7 (1), 9 (8), 60 (1), 101 (4), 103 (5), 201C (3), 301 (2), 335 (2).

The 29 specimens of this species included 22 sacconereis and 7 polybostrichus forms. Most of the females bore eggs on their incurved ventral surfaces. All but

one of the specimens were collected in Ungava Bay, the other individual having been taken in Jackman Sound, southern Frobisher Bay. Thus the distributions of this species and of *A. prismaticus* appear to be almost identical in the *Calanus* region. Also the collection dates of this species are similar to those of *A. prismaticus*, all of the 27 Ungava Bay specimens having been taken between June 24 and August 2. It appears that the planktonic stages of *A. verrilli* too are most abundant in Ungava Bay in early July.

Nereidae

Nereis pelagica L.

Fauvel, 1923, p. 336, fig. 130.

Canadian arctic: Packard (1863), Labrador (*Heteronereis arctica*); Packard (1867), Labrador; Verrill (1879), Cumberland Sound; Chamberlin (1920), Burwell, King George's Sound, Bernard Harbour; Treadwell (1937), Labrador, Southampton Island, Foxe Basin, Melville Peninsula; Berkeley and Berkeley (1943), Diana Bay, Wakeham Bay, Sugluk; the Berkeleys (pers. comm.), Somerset Island.

Further distribution: Cosmopolitan.

Collections: 18 (4), 25 (1), 27 (1), 28 (3), 30 (3), 33 (4), 58 (8), 64 (1, epitokous), 103 (4, including 1 epitokous), 107 (7), 123 (1, epitokous), 124 (26, epitokous), 126 (2), 203 (4), 208 (3), 210 (5), 217 (1, epitokous), 225 (2), 226 (60), 317 (7), 406 (6), 413 (1), 418 (1).

In addition to these, 145 atokous specimens were taken from the Atlantic cod (*Gadus callarias*) at Burwell, and 2 epitokous forms were collected in the same way.

In all, 32 epitokous forms were collected, between July 4 and August 20. On August 20, 1949, 26 epitokous specimens were taken in a single surface plankton tow at station 124. Notable among the epitokous forms were 2 specimens taken from the cod. Both showed, in place of the usual paired prostomial tentacles, a single tentacle, tapering to a point from a wide base. In all other respects both of these individuals agreed well with descriptions of this species, so are considered as abnormal forms of *Nereis pelagica*. A similar condition was reported in the Californian species *Nereis neonigripes* by Hartman (1936, p. 471, fig. 48f).

Nereis zonata Malmgren

Fauvel, 1923, p. 338, fig. 130.

Canadian arctic: McIntosh (1879), Ellesmere Island; Ditlevsen (1937), Jones Sound; Berkeley and Berkeley (1943), Hudson Bay.

Further distribution: Widely spread in arctic, subarctic and more southern waters, this species is probably circumpolar. In the eastern Atlantic area it is found south to the Mediterranean, but along the North American coasts it has not been recorded south of the *Calanus* region in the east, or south of Alaska in the West. While it is considerably more common than *Nereis pelagica* in West Greenland, it appears to be much less abundant in northern Canada.

Collection: Ogac Lake (3).

Nephthydidae

Nephthys ciliata O. F. Müller

Fauvel, 1923, p. 371, fig. 145.

Canadian arctic: Sabine (1824), North Georgian Islands (*Nais ciliata*); Ditlevsen (1909), Ellesmere Island; Chamberlin (1920), Dolphin and Union Strait; Ditlevsen (1937), Jones Sound; Treadwell (1937), Melville Peninsula; Berkeley and Berkeley (1943), Hudson Bay.

Further distribution: Probably circumpolar, in arctic, subarctic and more southern regions.

Collections: 20 and 21 (2), 33 (11), Burwell (1, from stomach of *Gadus callarias*), 102 (10), 107 (6), 201C (12), 222 (2), 231 (69), 416 (4).

Nephthys ?longosetosa Oersted

Fauvel, 1923, p. 367, fig. 143.

Canadian arctic: Packard (1867), Labrador (*N. longisetosa*), Berkeley and Berkeley (1943), Hudson Bay.

Further distribution: This species is recorded from West and East Greenland, Iceland and the Faroes (Wesenberg-Lund, 1953), northern Russia (Zatsepin, 1948), south in the Atlantic to the English Channel (Wesenberg-Lund, 1950), and to New England (Treadwell, 1948), and south to Panama along the western American coast (Berkeley and Berkeley, 1948).

Collection: 231 (1). This single specimen was incomplete and could not be identified with certainty.

Sphaerodoridae

Ephesia gracilis Rathke

Fauvel, 1923, p. 377, fig. 148.

Canadian arctic: Ditlevsen (1909), Ellesmere Island; Berkeley and Berkeley (1944), Dease Strait.

Further distribution: Possibly circumpolar, found chiefly in arctic and subarctic waters and as far south as the Mediterranean.

Collections: 18 (1), 102 (1), 319 (1).

Glyceridae

Glycera capitata Oersted

Fauvel, 1923, p. 385, fig. 151.

Canadian arctic: Ditlevsen (1909), Ellesmere Island; Ditlevsen (1937), Jones Sound.

Further distribution: Cosmopolitan.

Collections: 103 (1), Ogac Lake (1).

Onuphidae

Onuphis conchylega M. Sars

Fauvel, 1923, p. 415, fig. 164.

Canadian arctic: Packard (1867), Labrador (*O. eschrichtii*); Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador (*Nothria conchylega*); Chamberlin (1920), Dolphin and Union Strait; Ditlevsen (1937), Exeter Sound, Jones Sound; Treadwell (1937), Jones Sound; Berkeley and Berkeley (1944), Dease Strait.

Further distribution: Probably circumpolar, in arctic, subarctic and more southern regions.

Collections: 107 (2), 126 (1), 226 (1).

LUMBRINEREIDAE

Lumbrinereis fragilis (O. F. Müller)

Fauvel, 1923, p. 430, fig. 171.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*Lumbriconereis fragilis*); Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Hudson Bay; Ditlevsen (1937), Jones Sound (*Lumbriconereis fragilis*); Treadwell (1937), Labrador (*Lumbriconereis fragilis*); Berkeley and Berkeley (1943), Wakeham Bay, Hudson Bay.

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 40 (1), 102 (30), 107 (1), 201C (2), 212 (2), 222 (3), 231 (16), 416 (1).

ARICIIDAE

Scoloplos armiger (O. F. Müller)

Fauvel, 1927, p. 20, fig. 16.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island (*Aricia armiger*); Moore (1909), Labrador.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 51 (1), 102 (3), 107 (1), 216 (2), 310 (3), 413 (1), 416 (1), A6 (1), A8 (3), A9 (2), A12 (7), A20 (18).

Haploscoloplos elongata (Johnson)

Johnson, 1901, p. 412, pl. X, figs. 105–110.

CANADIAN ARCTIC: the Berkeleys (pers. comm.), Cumberland Sound.

FURTHER DISTRIBUTION: This is a Pacific species, recorded from Alaska to California (Berkeley and Berkeley, 1952). Taken neither by the *Calanus* nor by Ellis, this species was collected at Pangnirtung in 1937 and was identified by the Berkeleys.

SPIONIDAE

Spio filicornis (O. F. Müller)

Fauvel, 1927, p. 43, fig. 15.

CANADIAN ARCTIC: Berkeley and Berkeley (1943), Diana Bay, Wakeham Bay, Nottingham Island.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 31 (19), A8 (1), A27 (1).

Polydora caeca (Oersted)

Fauvel, 1927, p. 52, fig. 18.

CANADIAN ARCTIC: Berkeley and Berkeley (1943), Wakeham Bay.

FURTHER DISTRIBUTION: Predominantly a boreal and more southern species, it is recorded from only a few locations farther north, West Greenland, East Greenland, Jan Mayen, Spitzbergen (Wesenberg-Lund, 1953) and northern Russia (Zatsepin, 1948).

COLLECTIONS: A14 (1). Also a single specimen was taken by the *Calanus*, but the label was lost. However, as it was taken in 1952, it was collected either in Frobisher Bay or Cumberland Sound.

CIRRATULIDAE

Chaetozone setosa Malmgren

Fauvel, 1927, p. 101, fig. 35.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador.

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern regions.

COLLECTIONS: 13 (1), 20 and 21 (2), 94 (1), 102 (3), 234 (1), 319 (1), 416 (7).

Cirratulus cirratus (O. F. Müller)

Fauvel, 1927, p. 94, fig. 33.

CANADIAN ARCTIC: Packard (1867), Labrador; Ditlevsen (1909), Devon Island, Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Bernard Harbour; Ditlevsen (1937), Jones Sound; Berkeley and Berkeley (1943), Burwell, Wakeham Bay.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 322 (1), 402 (2), A26b (1).

CHLORAEMIDAE

Flabelligera affinis M. Sars

Fauvel, 1927, p. 113, fig. 40.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Bernard Harbour, Dolphin and Union Strait; Berkeley and Berkeley (1943), Nottingham Island, Hudson Bay; the Berkeleys (pers. comm.), Lake Harbour.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 203 (1), 322 (1), A44c (1).

Stylarioides plumosa (O. F. Müller)

Fauvel, 1927, p. 116, fig. 41.

CANADIAN ARCTIC: Packard (1863; 1867), Labrador (*Siphonostomum plumosum*); Ditlevsen (1909), Ellesmere Island (*Trophonia plumosa*); Ditlevsen (1937), Exeter Sound, Jones Sound.

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern regions.

COLLECTIONS: 44 (2, from stomachs of *Gadus callarias*); 102 (1), 107 (1), 224 (1, from stomach of *Gadus callarias*), 406 (1).

Brada inhabilis (Rathke)

Malmgren, 1867, p. 85, pl. XII, fig. 71 (*B. granulata*).

CANADIAN ARCTIC: Moore (1909), Labrador (*B. granulata*); Ditlevsen (1937), Exeter Sound, Jones Sound (*B. granulata*).

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern waters.

COLLECTION: A26b (1).

SCALIBREGMIDAE

Scalibregma inflatum Rathke

Fauvel, 1927, p. 123, fig. 44.

CANADIAN ARCTIC: Ditlevsen (1937), Exeter Sound.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 40 (1), 101 (2), 102 (2), 216 (4), 412 (1), A8 (1), A12 (4), A26 (2).

Eumenia crassa Oersted

Fauvel, 1927, p. 127, fig. 45.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island.

FURTHER DISTRIBUTION: A predominantly boreal species of the Atlantic, it extends into the subarctic and arctic north of the Atlantic.

COLLECTIONS: 203 (1), A12 (1).

OPHELIIDAE

Travisia forbesii Johnston

Fauvel, 1927, p. 138, fig. 48.

CANADIAN ARCTIC: Chamberlin (1920), Bathurst Inlet; the Berkeleys (pers. comm.), Lake Harbour.

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern regions.

COLLECTION: 40 (1).

Ophelia limacina (Rathke)

Tebble, 1952, p. 561.

CANADIAN ARCTIC: Treadwell (1937), Cobourg Island; Berkeley and Berkeley (1943), Wakeham Bay, Hudson Bay; the Berkeleys (pers. comm.), Cumberland Sound, ?Lake Harbour.

FURTHER DISTRIBUTION: Possible circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 210 (2), 217 (2), 417 (1), A43 (2).

Tebble (1952) re-established *Ophelia borealis* Quatrefages and *O. rathkei* McIntosh, 2 species formerly considered by many as being synonyms of *O. limacina* (Rathke). In view of this work it becomes necessary to re-examine specimens recorded as *O. limacina* before the distribution of this species can be made clear.

Ammotrypane aulogaster Rathke

Fauvel, 1927, p. 133, fig. 47.

CANADIAN ARCTIC: Fewkes (1888) and Ditlevsen (1909), Ellesmere Island.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 20 and 21 (1), 107 (1), 216 (8).

CAPITELLIDAE

Capitella capitata (Fabricius)

Fauvel, 1927, p. 154, fig. 55.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island; Chamberlin (1920), Bernard Harbour; Berkeley and Berkeley (1943), Diana Bay, Wakeham Bay, Nottingham Island, Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 94 (1), 229 (1), 412 (3), 418 (1), A6 (4), A8 (3), A8h (1), A9 (6), A12 (2), A15 (1), A17 (1), A20 (5).

ARENICOLIDAE

Arenicola marina (L.)

Ashworth, 1910, p. 5, fig. 1.

CANADIAN ARCTIC: Packard (1867), Labrador; Berkeley and Berkeley (1943), Hudson Bay. This species was reported by Chamberlin (1920) from Bernard Harbour, but the specimens later were shown by Ashworth (1924) to be *A. glacialis* Murdoch.

FURTHER DISTRIBUTION: Mainly of boreal and more southern distribution, it extends north of the Atlantic to West and East Greenland, Spitzbergen and northern Russia.

COLLECTIONS: 64 (3), 412 (1), A32 (several fragments, not definitely identified).

MALDANIDAE

Nichomache lumbricalis (Fabricius)

Ardwidsson, 1906, p. 86, pl. VIII, figs. 244–245.

CANADIAN ARCTIC: Packard (1867), Labrador.

FURTHER DISTRIBUTION: Possibly circumpolar, predominantly arctic and subarctic.

COLLECTION: 222 (3).

Axiothella catenata (Malmgren)

Malmgren, 1867, p. 99, pl. X, fig. 59 (*Axiothea catenata*).

CANADIAN ARCTIC: Chamberlin (1920), Burwell (*Paraxiothea catenata*); Berkeley and Berkeley (1943), Nottingham Island.

FURTHER DISTRIBUTION: Probably circumpolar, chiefly in subarctic waters.

COLLECTION: 216 (1).

Maldane sarsi Malmgren

Arwidsson, 1906, p. 251, pl. VI, figs. 192–199.

CANADIAN ARCTIC: Moore (1909), Labrador; Berkeley and Berkeley (1943), Burwell.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 102 (1), 107 (1), 201C (3), 231 (11), 416 (8).

OWENIIDAE

Owenia fusiformis Delle Chiaje

Fauvel, 1927, p. 203, fig. 71.

CANADIAN ARCTIC: Berkeley and Berkeley (1943), Nottingham Island (*Ammochares fusiformis*). Whiteaves (1885) recorded *Ammochares* sp. from Burwell.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 107 (2), 231 (3).

AMPHICTENIDAE

Cistenides granulata (L.)

Nilsson, 1928, p. 28, fig. 8 (*Pectinaria granulata*).

CANADIAN ARCTIC: Packard (1863), Labrador (*Pectinaria eschrichtii*); Packard (1867), Labrador; McIntosh (1879), Ellesmere Island; Verrill (1879), Cumberland Sound; Whiteaves (1885), Ashe Inlet (*Pectinaria granulata*); Chamberlin (1920), Hudson Bay, Bernard Harbour, Dolphin and Union Strait; Ditlevsen (1937), Exeter Sound (*Pectinaria granulata*); Treadwell (1937), Melville Peninsula (*Pectinaria granulata*); Berkeley and Berkeley (1943), Hudson Bay; Berkeley and Berkeley (1944), Bernard Harbour; the Berkeleys (pers. comm.), Lake Harbour.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 33 (1), 203 (1), 317 (2), 318 (1), 319 (1), 321 (1), 404 (1), 406 (3), 413 (1), 418 (1), Ogac Lake (7), Ogac Lake (*c.* 200, from stomachs of *Gadus callarias*); Koksoak River mouth (1, from stomach of bearded seal, *Erignathus barbatus*), Whale River (1, from stomach of bearded seal), head of Frobisher Bay (12, from stomach of ringed seal, *Phoca hispida*), A9 (1), A32 (1), A44 (1), A44c (2).

This species seems to be much more abundant in the northern part of the *Calanus* region than in Ungava Bay. Of some 240 specimens taken only 4 originated in Ungava Bay, all the others coming from north of Hudson Strait.

Counts made on the paleae of 11 individuals showed a range of from 7 to 9 on each side. Scaphal setae counts on 10 specimens varied from 8 to 12 per side.

Cistenides hyperborea Malmgren

Malmgren, 1865, p. 360, pl. XVIII, fig. 40.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island (*Pectinaria hyperborea*); Moore (1909), Labrador (*Pectinaria hyperborea*); Berkeley and Berkeley (1943), Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 231 (2), 329 (5), 416 (1).

This species is apparently far from being as abundant as *C. granulata* in northern Canadian waters. It appears also to be restricted to deeper water than the former species.

Counts made on 8 individuals showed the number of paleae ranging from 10 to 14 on each side, and the number of scaphal setae varying from 6 to 10 per side.

Ampharetidae

Ampharete grubei Malmgren

Fauvel, 1927, p. 227, fig. 79.

Canadian arctic: Packard (1867), Labrador.

Further distribution: Probably circumpolar, in arctic, subarctic and more southern waters.

Collections: 33 (1), 40 (1), 51 (1), 231 (1), 317 (1), A6 (5), A8 (1), A9 (9), A20 (3).

Ampharete arctica Malmgren

Malmgren, 1865, p. 364, pl. XXVI, fig. 77.

Canadian arctic: Berkeley and Berkeley (1943), Nottingham Island.

Further distribution: Circumpolar, predominantly of subarctic areas.

Collection: 416 (1).

Amphicteis sundevalli Malmgren

Malmgren, 1865, p. 366, pl. XXV, fig. 73.

Canadian arctic: McIntosh (1879), Ellesmere Island.

Further distribution: East and West Greenland, common only at Spitzbergen (Wesenberg-Lund, 1953), northern Russia (Zatsepin, 1948).

Collections: 102 (3), 231 (1).

Pseudosabellides littoralis Berkeley

Berkeley and Berkeley, 1943, p. 131.

Canadian arctic: Berkeley and Berkeley (1943), Burwell, Diana Bay, Wakeham Bay.

Further distribution: This species is known elsewhere only from eastern Vancouver Island (Berkeley and Berkeley, 1952).

Collections: 33 (1), Burwell (1), 203 (1), 310 (1), 402 (2), A20 (1), A26 (3).

This species is recorded here from Ungava Bay, Frobisher Bay and the coast between Frobisher Bay and Cumberland Sound, by 10 individuals. While previous records of the species are all from the intertidal region, specimens were found by the *Calanus* as deep as 30 metres.

Pseudosabellides lineata Berkeley

Berkeley and Berkeley, 1943, p. 131.

Canadian arctic: Berkeley and Berkeley (1943), Burwell, Nottingham Island; Berkeley and Berkeley (1944), Dease Strait.

Further distribution: Elsewhere this species is recorded only from Alaska and from Vancouver Island (Berkeley and Berkeley, 1952).

Collection: 102 (1).

Lysippe labiata Malmgren

Malmgren, 1865, p. 367, pl. XXVI, fig. 78.

Canadian arctic: No previous record.

Further distribution: West and East Greenland, Spitzbergen, Kara Sea, Novaya Zemlya,

Iceland, Scandinavia, Denmark (Wesenberg-Lund, 1953), New England (Verrill, 1881, *L. lobata*), Alaska and British Columbia (Berkeley and Berkeley, 1952).

COLLECTIONS: 102 (1), 231 (1).

Melinna cristata (M. Sars)

Fauvel, 1927, p. 237, fig. 83.

CANADIAN ARCTIC: Berkeley and Berkeley (1943), Hudson Bay.

FURTHER DISTRIBUTION: Possibly circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 107 (1), 231 (3).

TEREBELLIDAE

Amphitrite cirrata O. F. Müller

Fauvel, 1927, p. 251, fig. 86.

CANADIAN ARCTIC: Packard (1867), Labrador; Ditlevsen (1909), Ellesmere Island; Chamberlin (1920), Burwell.

FURTHER DISTRIBUTION: Possibly circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 20 and 21 (1), 226 (1), 406 (1), Gyrfalcon Islands (12, from stomach of bearded seal, *Erignathus barbatus*), A12c (2).

Amphitrite groenlandica Malmgren

Fauvel, 1927, p. 250, fig. 86.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: This species is confined largely to arctic and subarctic areas of the Atlantic, and is recorded in North America from New England (Verrill, 1881).

COLLECTION: 201C (1).

Amphitrite affinis Malmgren

Fauvel, 1927, p. 246, fig. 84.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: This species is found in arctic, subarctic and more southern waters. In North America it has been recorded from New England (Verrill, 1881, *A. intermedia*).

COLLECTION: A9 (2).

While these 2 individuals differ in certain respects from published descriptions of *Amphitrite affinis*, they are placed in this species. The larger individual is about 90 mm. long, the smaller, incomplete, slightly shorter. Both have 13 rather than 17 thoracic bristle-bearing segments, and both have only 2 rather than 3 pairs of gills. Posterior to the thirteenth chaetigerous segment the ventral tori of the next 4 segments bear 2 rows of uncini, posterior to which they assume the characteristics of abdominal tori, having only one row of uncini. Thus it appears that in these specimens dorsal chaetae have failed to develop in the 4 posterior thoracic segments, although all other features of this region comply with descriptions given for this species. Only the first 2 pairs of gills are present, and these differ from Fauvel's figure (which is, however, of the third and thus the largest pair) only in having fewer ramifications. Apart from these characters these specimens show excellent agreement with this species, and therefore are referred to as aberrant individuals of *Amphitrite affinis*.

Nicolea zostericola (Oersted)

Fauvel, 1927, p. 261, fig. 90.

CANADIAN ARCTIC: Ditlevsen (1909), Devon Island, Ellesmere Island; Moore (1909), Labrador; Chamberlin (1920), Bernard Harbour (*N. venustula*); Berkeley and Berkeley (1943), Wakeham Bay, Nottingham Island; Berkeley and Berkeley (1944), Bernard Harbour, Coronation Gulf.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 18 (1), 58 (1), 319 (1), 331 (1), 333 (1), 418 (1), A26 (1).

Pista maculata (Dalyell)

Fauvel, 1927, p. 263, fig. 91.

CANADIAN ARCTIC: McIntosh (1879) and Ditlevsen (1909), Ellesmere Island (*Scione lobata*); Ditlevsen (1937), Jones Sound (*Scione lobata*); Berkeley and Berkeley (1943), Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, principally of arctic and subarctic waters.

COLLECTIONS: 13 (2), 33 (3), 103 (4), 329 (1).

Pista cristata (Müller)

Fauvel, 1927, p. 266, fig. 93.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island.

FURTHER DISTRIBUTION: This species is recorded from neither West nor East Greenland. It occurs in Iceland (Wesenberg-Lund, 1951), Spitzbergen (Augener, 1928), northern Russian seas (Zatsepin, 1948), south Atlantic and Antarctic (Fauvel, 1927), and in North America from Alaska to California (Berkeley and Berkeley, 1952), in the Gulf of St. Lawrence (Treadwell, 1948) and in New England and south to Virginia (Verrill, 1881).

COLLECTION: A12 (2).

In these 2 specimens only one pair of gills was present in each, in one the right, and in the other the left being considerably the larger.

Pista flexuosa (Grube)

Malmgren, 1865, p. 384, pl. XXIV, fig. 68 (*Axionice flexuosa*).

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*Axione flexuosa*); Ditlevsen (1909), Ellesmere Island (*Axionice flexuosa*); Moore (1909), Labrador (*Axionice flexuosa*).

FURTHER DISTRIBUTION: Circumpolar, predominantly of arctic and subarctic waters.

COLLECTION: 203 (1).

Laphania boecki Malmgren

Fauvel, 1927, p. 269, fig. 94.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: This species is found in arctic, subarctic and more southern waters. It is not recorded from West Greenland. The only North American record appears to be from the Gulf of St. Lawrence (McIntosh, 1922).

Leaena abranchiata Malmgren

Malmgren, 1865, p. 385, pl. XXIV, fig. 64.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador; Berkeley and Berkeley (1943), Wakeham Bay.

FURTHER DISTRIBUTION: Possibly circumpolar, predominantly an arctic and subarctic species.

COLLECTIONS: A20a (1), A23 (5), A26 (1).

Thelepus cincinnatus (Fabricius)

Fauvel, 1927, p. 271, fig. 95.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*T. circinnatus*); Verrill (1879), Cumberland Sound; Whiteaves (1885), Burwell (*T. circinatus*); Ditlevsen (1909), Devon Island, Ellesmere Island (*T. circinnatus*); Moore (1909), Labrador; Chamberlin (1920), King George's Sound; Ditlevsen (1937), Jones Sound; Treadwell (1937), Hudson Strait, Melville Peninsula, Fury and Hecla Strait, Jones Sound.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 25 (1), 27 (2), 30 (2), 103 (3), 106 (1), 107 (1), 126 (3), 206 (1), 208 (3), 210 (2), 222 (2), 226 (19), 317 (5), 319 (15), 321 (1), 404 (1), 406 (1), 413 (2).

Lysilla lovéni Malmgren

Wesenberg-Lund, 1934, p. 26, figs. 7–8.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: East Greenland, western Norway, Faroes, Shetlands, Finmark (Wesenberg-Lund, 1953), North Sea (Fauvel, 1927). It appears not to have been recorded formerly from North America.

COLLECTIONS: 102 (1), 416 (1).

Terebellides stroemi M. Sars

Fauvel, 1927, p. 291, fig. 100.

CANADIAN ARCTIC: Ditlevsen (1909), Ellesmere Island; Moore (1909), Labrador; Treadwell (1937), Melville Peninsula; Berkeley and Berkeley (1943), Burwell.

FURTHER DISTRIBUTION: Cosmopolitan.

COLLECTIONS: 102 (6), 107 (1), 201C (1), 231 (8), 416 (7).

SABELLIDAE

Sabella fabricii Kröyer

Fauvel, 1927, p. 300, fig. 103.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island (*S. spetzbergensis*); Ditlevsen (1909), Ellesmere Island; Berkeley and Berkeley (1943), Wakeham Bay (*S. crassicornis*).

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 33 (2), 103 (1), 203 (1), 225 (1), 317 (1), A20a (1).

Potamilla neglecta (M. Sars)

Malmgren, 1865, p. 401, pl. XXVII, fig. 84.

CANADIAN ARCTIC: No previous record.

FURTHER DISTRIBUTION: Possibly circumpolar, of predominantly arctic and subarctic distribution.

COLLECTION: 334 (1).

Chone infundibuliformis Kröyer

Fauvel, 1927, p. 334, fig. 116.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island; Ditlevsen (1909), Ellesmere Island; Ditlevsen (1937), Jones Sound; Berkeley and Berkeley (1943), Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 20 and 21 (1), 28 (1), 102 (2), 203 (1), 208 (1), 334 (1), 406 (1).

Euchone analis (Kröyer)

Malmgren, 1867, p. 114, pl. XIII, fig. 80.

CANADIAN ARCTIC: McIntosh (1879), Ellesmere Island; Chamberlin (1920), Bernard

Harbour; Berkeley and Berkeley (1943), Burwell, Wakeham Bay; Berkeley and Berkeley (pers. comm.), Cumberland Sound.

FURTHER DISTRIBUTION: Circumpolar, mainly of arctic and subarctic regions.

COLLECTIONS: 203 (1), 412 (6), A9 (1), A14 (2), A23 (1).

Fabricia sabella (Ehrenberg)

Fauvel, 1927, p. 325, fig. 113.

CANADIAN ARCTIC: Berkeley and Berkeley (1943), Diana Bay.

FURTHER DISTRIBUTION: It occurs in arctic, subarctic and boreal regions of the Atlantic (Wesenberg-Lund, 1953), in North America south to Vancouver Island (Berkeley and Berkeley, 1952), and to New England (Verrill, 1881, *F. stellaris*).

COLLECTION: 413 (1).

SERPULIDAE

Spirorbis spirillum (L.)

Fauvel, 1927, p. 392, fig. 132.

CANADIAN ARCTIC: Packard (1863; 1867), Labrador; Verrill (1879), Cumberland Sound (*S. lucidus*); Moore (1909), Labrador; Chamberlin (1920), Burwell, Bernard Harbour, Dolphin and Union Strait (*Circeis spirillum*); Treadwell (1937), Southampton Island; Berkeley and Berkeley (1943), Burwell, Wakeham Bay, Diana Bay, Sugluk, Nottingham Island, Hudson Bay.

FURTHER DISTRIBUTION: Circumpolar, in arctic, subarctic and more southern waters.

COLLECTIONS: 217 (12), A7 (3), A8h (2), A9f (7), A17 (1).

This species is almost certainly more abundant than these collections would suggest. Many small serpulids collected in the field, on rocks and plants, were not retained, and many of the tubes were broken or empty.

Spirorbis borealis Daudin

Fauvel, 1927, p. 399, fig. 135.

CANADIAN ARCTIC: Packard (1863), Labrador (*S. nautiloides*); Chamberlin (1920), Dolphin and Union Strait (*S. spirorbis*); Ditlevsen (1937), Exeter Sound (*S. spirorbis*).

FURTHER DISTRIBUTION: Probably circumpolar, in arctic, subarctic and more southern waters.

COLLECTION: 319 (1).

ZOOGEOGRAPHICAL CONSIDERATIONS

The polychaetous annelids are characterized by the extremely widespread distribution of many of the species of the group, and, in fact, they appear to be unique among marine invertebrates in the degree to which this characteristic is shown. Great variability in methods of reproduction and development has been suggested as one factor instrumental in permitting such wide dispersion.

Of the 74 species discussed here, 42 species (56.7%) are circumpolar or probably so. Nine species (12.2%) are referred to as cosmopolitan. Five species (6.8%) are found north of the Atlantic and as far west as Alaska or the Bering Sea, but not in the Pacific. Five species (6.8%) are confined to the region north of the Atlantic. Three species (4.1%) are recorded elsewhere only from the western Canadian arctic, Alaska or the Pacific. Some 49 species (66.2%) occupy an arctic, subarctic and boreal range, at least, and only 15 species (20.3%) are predominantly arctic and subarctic in distribution.

The polychaetes of the eastern Canadian arctic show a close relationship with those of West Greenland, and with the entire arctic-subarctic region north of the Atlantic. Of 134 known eastern arctic species, 98 (73%) are recorded from West Greenland, 93 (69%) from Spitzbergen, 89 (66%) from northern U.S.S.R., and 82 (61%) from East Greenland.

A much less close relationship is shown with Alaska, where 54 eastern arctic species (40%) have been recorded. However, a Pacific faunal element is present which comprises nearly 6% of the eastern arctic species. The following 8 species recorded from the eastern arctic are reported elsewhere only from the Pacific (except *Pseudosabellides lineata* Berkeley, which has been taken also in the western Canadian arctic):

Eunoe depressa Moore, *Evarnella triannulata* (Moore), *Eulalia levicornuta* Moore, *Haploscoloplos elongata* (Johnson), *H. kerguelensis* (McIntosh), *Pseudosabellides littoralis* Berkeley, *P. lineata* Berkeley and *Scionella estevanica* Berkeley.

In the 134 known species of polychaetes of the Canadian eastern arctic, the predominantly arctic-subarctic element ranges from 14 species (23.0% of the 61 known species) in the Ellesmere Island–Jones Sound region to only 5 species (9.1% of the 55 known species) in Labrador and 2 species (8.3% of the 24 known species) in Hudson Bay. The following 21 (15.7%) eastern arctic species are predominantly arctic and subarctic in distribution:

Harmothoe senta (Moore), *H. badia* (Théel), *Melaenis lovéni* Malmgren, *Castalia aphroditoides* (Fabricius), *Paranaitis wahlbergi* Malmgren, *Syllis fasciata* Malmgren, *Autolytus prismaticus* (Fabricius), *A. verrilli* Marenzeller, *Nichomache lumbricalis* Malmgren, *Axiothella catenata* (Malmgren), *Ampharete arctica* Malmgren, *Amphicteis sundevalli* Malmgren, *Lysippe labiata* Malmgren, *Glyphonostomum palescens* (Théel), *Amphitrite groenlandica* Malmgren, *Pista maculata* (Dalyell), *P. flexuosa* (Grube), *Leaena abranchiata* Malmgren, *Potamilla neglecta* (Sars), *Dasychone infarcta* Kröyer and *Euchone analis* (Kröyer).

The following 9 notably southern species are recorded from the Canadian eastern arctic: *Tomopteris planktonis* Apstein (North Atlantic and south), *Syllis hyalina* Grube (North Atlantic, British Columbia and south), *Lumbrinereis hebes* Verrill (New England), *Tharyx acutus* Webster and Benedict (Maine), *Brada granosa* Stimpson (Gulf of St. Lawrence and south), *Stylarioides aspera* (Stimpson) (Bay of Fundy and south), *Praxillella affinis* (Sars) (south Norway and south), *Spirorbis validus* Verrill (Nova Scotia and south, Alaska) and *S. pagenstecheri* Quatrefages (North Sea and south).

Of these 9 species, all but *Brada granosa*, which is recorded from Jones Sound, are reported only from the southern part of the eastern arctic area (Labrador, Ungava Bay and eastern Hudson Strait), and all but *Brada granosa*, *Syllis hyalina* and *Praxillella affinis* are recorded only from Labrador and the northeastern corner of Ungava Bay.

SUMMARY

1. The material consists of some 1,800 specimens representing 74 species of polychaetous annelids, the majority of which were collected by the *Calanus*

expeditions of 1947–1952, in Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound. Additional specimens were obtained from Frobisher Bay, Cumberland Sound, Padloping Island and intermediate waters, and a list of 9 species from Hudson Strait, Cumberland Sound and Somerset Island, identified by E. and C. Berkeley, is included.

2. Two species are new records for North America and 12 species are new for the Canadian eastern arctic, bringing the known polychaete fauna of this region to at least 134 species.

3. It is apparent that the polychaete fauna of the eastern Canadian arctic shows a closer relationship to that of west Greenland and to the entire arctic-subarctic region north of the Atlantic, than to Alaska and the Pacific. However, a Pacific faunal element is present which comprises nearly 6% of the eastern arctic species. The extent of the predominantly arctic-subarctic element in the fauna diminishes generally from north to south, and is found in its lowest concentration in Hudson Bay. Distinctly southern invaders within the fauna are limited almost entirely to the southernmost part of the region, Labrador and northeastern Ungava Bay.

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Contrasting Susceptibilities of Two Fish Species to a Diet Destructive to Vitamin B_1[1]

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ABSTRACT

Specimens of *Schilbeodes mollis*, a catfish, and of *Enneacanthus obesus*, a sunfish, were fed exclusively on carp eggs. Within a month, catfish developed symptoms of athiaminosis and died. These results were swifter and more widespread under longer, brighter light. Survivors responded to a change of diet with the addition of thiamin chloride hydrochloride. No sunfish showed any signs of athiaminosis or died. Sunfish subjected to long, bright light were induced to spawn out of season. Catfish on a carp-egg-free diet for 10½ weeks from date of capture remained healthy without the addition of thiamin chloride.

INTRODUCTION

Diets of raw carp viscera and of the viscera of certain other fish species have produced athiaminosis in trout, chicks, pigeons, rats, cats and foxes (Yudkin, 1949), with clinical symptoms of Chastek paralysis, a polyneuritic condition resembling Wernicke's disease (Green *et al.*, 1941).

The dietary data here presented are incidental to some experiments (Harrington, in press) on effects of external physical factors upon reproduction in the banded sunfish, *Enneacanthus obesus* (Girard), and in an ameiurid fish, the tadpole madtom, *Schilbeodes mollis* (Herman). Fish eggs proved an easily administered food for these two diminutive species, few individuals of which greatly exceed 3 inches in total length. Both species were fed carp (*Cyprinus carpio*) eggs for extended periods of time (see below and Table I). Carp ovaries were kept frozen, and eggs in small lots were thawed before feeding. Tap water was used in the aquaria, and was further filtered continuously through activated charcoal, so that it could be expected to provide thiamin only briefly and in negligible amounts. Connecticut lake water contains from 0.03 to 1.2 micrograms of thiamin per liter, of which all but from 7% to 39% can be removed by filtration (Hutchinson, 1943). Carp eggs were selected in ignorance of the fact that carp viscera are rich in thiaminase, an enzyme destructive to vitamin B_1. Some consequences of this ill-advised diet, which may prove heuristic in the comparative physiology of thiamin and of thiaminase, are considered.

SUNFISH FEEDING EXPERIMENTS

Banded sunfish, half of them subjected to 15 hours of daily light (fall daylight supplemented by overlapping increments of artificial illumination), the other half merely to fall daylight, were fed for as long as 72 days on an exclusively carp-egg

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diet. They ate voraciously with no diminution in feeding to the time the last fish were sacrificed. There were no signs of even the earliest symptoms of Chastek paralysis, anorexia, hyperesthesia and loss of balance (cf. Yudkin, 1949). A total of 29 fish were placed on the carp-egg diet, beginning October 4, 1950. These 29 fish were sacrificed in three lots, on different days subsequent to the introduction of the carp-egg diet, as follows: 12 (48th–49th day), 3 (51st–55th day), 14 (72nd day). There were no mortalities, and all fish were healthy at the time of sacrifice. Moreover, those sunfish given additional illumination advanced sexually from the quiescent, prespawning condition to complete functional maturity out of season, by the 45th day of the diet (November 17). During 13 of the ensuing 26 days, 163 spawning acts with 115 egg depositions were observed, and free swimming larvae hatched sporadically (Harrington, in press). Breeding fish spared to the 72nd day were undiminished in general vigour and sexual prowess.

Beerstecher (1950) has emphasized the fundamental role played by thiamin in metabolism, the greater thiamin requirements of the smaller animals with their higher metabolic rates, and the consistently greater requirements of cold- as compared with warm-blooded animals. Thiamin deprivation has resulted in testicular hypofunction in man (Best and Taylor, 1945) and in a decline in aggressiveness and in social status in rats (Beeman and Allee, 1945) and dogs (Berg, 1947). In the context of these very general considerations, it may be noted without any implied inferences that those sunfish which attained functional maturity spawned for almost a month not only outside of but presumably in addition to their normal period of spawning. The experimentally induced gonadal maturation entailed a doubling of egg diameters. The males departed abruptly from the passivity normal for the season to display a complex of intense and sustained breeding activities.

MADTOM FEEDING EXPERIMENTS

Tadpole madtoms fed exclusively on carp eggs began to sicken and die within a month (Tables I, II). Mortality was highest among those subjected to fall daylight with enough additional light of 15 or more watts' intensity to afford a total of 15 hours of daily light. Mortality was much lower among those kept in total darkness or subjected to 15 hours of daily light when the supplementary illumination was only 7½ watts. Before the symptoms of the dying fish were identified as those of Chastek paralysis, the possibility of a direct photodynamic effect was considered, but the higher mortality under longer, brighter light is more likely the function of a light-stimulated increase in metabolic rate. Of the fish on long, bright light, 73% died in 1951 by the 33rd day and 91.7% in 1952 by the 31st day. The total mortality of fish under all light conditions was 36% in 1951 (by the 85th day) and 54.3% in 1952 (by the 31st day).

The symptoms of the unhealthy fish were clearly those of Chastek paralysis as described for the trout (Alexander *et al.*, 1941). These madtoms exhibited loss of balance, lying on their sides, upside down and vertically (in the weeds). Before the onset of symptoms, feeding was so voracious that abdomens were

TABLE I. Mortality among 106 tadpole madtoms fed a diet of carp eggs, beginning September 21, 1951. Group 1 had 15 hours of light daily, consisting of daylight supplemented by the artificial illumination of a 50-watt bulb (yielding 8–20 foot-candles on the bottom of the dry aquarium). Group 2 had fall daylight for 38 days, then 15 hours of light daily consisting of daylight supplemented by a 7½-watt bulb (½–3 foot-candles). Group 3 was kept in total darkness.

	Group 1	Group 2	Group 3	Total
Allocation of fish	45	22	39	106
Died 27th–33rd day	33	..	4	37
	(73%)		(10%)	
Sacrificed 34th day	12	..	15	27
	(27%)		(38%)	
Died 79th–85th day	..	3	4	7
		(14%)	(10%)	
Sacrificed 87th–88th day	..	19	16	35
		(86%)	(41%)	
Total mortality	33	3	8	44
	(73%)	(14%)	(21%)	(36%)

distended, then feeding ceased abruptly. The fish developed hyperesthesia ("fright disease"). A slight noise, vibration or movement would send them dashing back and forth the length and height of a 40-gallon aquarium. The excitement of one fish was evidently communicated to the others. Often they would push one after the other under the bottom of a pile of their fellows so that the pile turned over continually. Finally, fish became paralysed and floated at the surface. Occasional tremors were observed. At the time of death, the body became mottled with pale-yellowish blotches, which seemed to represent localized contractions of chromatophores.

With the recognition of the symptoms as those of Chastek paralysis, an attempt was made in 1952 (Table III) to abate the disease and to restore to health the 21 fish surviving to the 35th day. The carp-egg diet was replaced by a diet of dried commercial aquarium food supplemented with enchytraeid worms. Also, thiamin chloride hydrochloride was added to the aquarium water, in the proportion of 1 cc. of a 100 mg. per cc. aqueous solution to 10 gallons of aquarium water, and filtration was suspended. When turbidity necessitated filtration, this

TABLE II. Mortality among 47 tadpole madtoms fed a diet of carp eggs, beginning October 1, 1952. Group 4 had 15 hours of light daily, consisting of daylight supplemented by a 15-watt bulb (yielding 2–5 foot-candles on the bottom of the dry aquarium). Group 5 was kept in total darkness.

	Group 4	Group 5	Total
Allocation of fish	24	23	47
Died 17th–31st day	22	4	26
	(92%)	(17%)	(54%)
Fish surviving 35th day	2	19	21
	(8%)	(83%)	(46%)

was followed by another application of thiamin accompanied by a period of non-filtration. The process was repeated four times in all.

Following the diet change and thiamin treatment, only 2 fish (7.3%) died, one 85, and the other 105 days later (Table III). Neither had shown the symptoms of Chastek paralysis. Seventy-six per cent of the fish were not sacrificed for 140 days (175 days since the beginning of their captivity). All were healthy at the time of sacrifice.

A further group of madtoms, collected May 25, 1953, were given a diet of earthworms supplemented with frozen mackerel eggs, beginning that day. Earthworms were chosen as a source of thiamin, since they among other invertebrates seem to contain more of this vitamin than do any vertebrates (Hutchinson, 1943; Woods *et al.*, 1942). Mackerel viscera are reported to be thiaminase-free (Neilands, 1947; Lieck and Ågren, 1944). All of the 32 madtoms maintained on this diet were kept in daylight (spring-summer). The total mortality was 1 fish (3.1%), which died on the 12th day without any symptoms of Chastek paralysis. Eight fish were sacrificed the 30th day, 13 on the 36th day, and the last 10 on the 74th day (August 7), all of them in excellent condition when sacrificed.

TABLE III. Mortality of fish surviving after 35 days of carp-egg diet, when changed to a thiaminase-free diet with thiamin hydrochloride added. Group 6 was illuminated in the same manner as Group 4 of Table II. Group 7 had 15 hours of light daily, consisting of daylight supplemented by a 7½-watt bulb (35th–105th day), by a 25-watt bulb (106th–145th day), and by a 60-watt bulb (10-27 foot-candles) thereafter. Group 8 was kept in total darkness.

	Group 6	Group 7	Group 8	Total
Reallocation of fish surviving on the 35th day	2	12	7	21
Died 120th day	..	..	1 (14%)	1
Died 154th day	..	1 (8%)	..	1
Sacrificed 150th day	..	1 (8%)	..	1
Sacrificed 170th day	2 (100%)	..	..	2
Sacrificed 175th day	..	10 (84%)	6 (86%)	16
Total mortality	0	1 (8%)	1 (14%)	2 (7%)

DISCUSSION OF RESULTS

The long-sustained (72 days) absence of any symptoms of athiaminosis in the banded sunfish on a thiaminase-rich diet, even when induced to mature and breed out of season, contrasts sharply with the effects of the same diet on tadpole madtoms, which began to sicken and die as early as the 17th day, the majority of deaths occurring within a month. In succumbing to thiaminase-induced B_1 avitaminosis, tadpole madtoms agree with trout (Wolf, 1942), with which they share the same symptoms (Alexander *et al.*, 1941).

It is tempting to speculate on the possible relation between these contrasting results and the distribution of thiaminase among fishes. Eighty-one fish species have been assayed for thiaminase (Wolf, 1942; Deutsch and Hasler, 1943; Lieck and Ågren, 1944; Yudkin, 1945; Neilands, 1947). Thirty-seven of the 50 freshwater species investigated contained thiaminase, 2 coregonid, 1 clupeid, 1 osmerid, 1 catostomid, 13 cyprinid, 3 ameiurid, 1 umbrid, 2 cyprinodontid, 1 gadid, 1 serranid and 1 percid species. It was found in only 2 out of 31 saltwater species, 1 clupeid and 1 belonid. The 23 freshwater species in which thiaminase was lacking comprised 5 salmonid, 3 coregonid, 1 cyprinid, 1 escoid, 1 anguillid, 1 gadid, 1 serranid, 6 centrarchid, and 4 percid species. The saltwater species lacking thiaminase included 2 clupeid, 1 osmerid, 1 scombrid, 2 labrid, 1 scorpaenid, 2 cottid, 1 cyclopterid, 2 triglid, 1 anarchidadid, 1 zoarcid, 1 merluciid, 7 gadid, 7 pleuronectid, and 1 lophiid species.

The viscera of neither banded sunfish nor tadpole madtoms have been assayed, but it is interesting to note that all six centrarchid species were thiaminase-free, whereas 17 of the 18 species of the order Ostariophysi (Catostomidae, Cyprinidae, Ameiuridae) contained thiaminase. On the other hand, all four species of trout were thiaminase-free. *Belone acus* and *Clupea harengus* were the only strictly marine species containing the enzyme, although the latter species has been reported to be lacking in thiaminase in European waters (Lieck and Ågren, 1944). This enzyme appears to be most consistently associated with the viscera of fishes of the order Ostariophysi, to have no obvious pattern of occurrence among other freshwater species, and to be found only rarely among saltwater species. It is conceivable that a few records, especially of predator species, may be in error owing to the presence of thiaminase-containing forage fish in the stomach contents.

The explanation of the contrasting susceptibilities of banded sunfish and tadpole madtoms to a thiaminase-rich diet is to be sought in the comparative physiology of vitamins and in vitamin biochemistry. Whether this contrast is an implication of the taxonomic distribution of thiaminase cannot be determined until there are more feeding experiments and more data on the distribution of thiaminase among both predator and forage fish and among forage invertebrates. The earlier onset in tadpole madtoms of the symptoms of athiaminosis with prolonged and brighter illumination suggests the importance of standardizing light conditions in such biological assays.

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Relation Between Feeding and the Sexual Cycle of the Haddock[1]

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ABSTRACT

As haddock (*Melanogrammus aeglifinus* (Linn.)) approach the spawning period they practically cease to take food. This fast is continued throughout the spawning period. On the completion of spawning the fast is broken and the haddock feed voraciously for a few weeks regaining weight lost as a result of spawning.

INTRODUCTION

The significant changes brought about in the rate of feeding among haddock (*Melanogrammus aeglifinus*) by the spawning act do not appear to have been especially considered by previous authors. There are references in the literature to the well-known observation that haddock and other fish apparently do not feed during the actual spawning period. There are several well-known cases of fish, such as lampreys, eels and Pacific salmon, ceasing to feed for a considerable time previous to spawning and refusing to take food during spawning. There are other instances in which fish do not eat for a certain period of time. Among anadromous species such as the smelt (*Osmerus mordax*) and the alewife (*Pomolobus pseudoharengus*) (Bigelow and Welsh, 1924), as well as the shad (*Alosa sapidissima*) (Leim, 1925), the cessation of feeding in fresh water during the spawning migration is known. Carr (1907 and 1909) observed high percentages of empty stomachs among such species as the common dab (*Pleuronectes limanda*), long rough dab (*Hippoglossus limandoides*), and the whiting (*Gadus merlangus*) during the winter months (December to March). She attributed this to the influence of low winter temperatures. Todd (1915) made extensive observations on the plaice (*Pleuronectes platessa*) in the North Sea and found that during the period from November to February there was a high percentage of empty stomachs (up to 100%). He did not agree with Carr's theory that low water temperatures were responsible for cessation of feeding but stated that "this winter fast is very probably due to the advent of the spawning season". It must be noted that Russell (1914) made the statement "there is no cessation of feeding during the winter". None of the above authors correlated their observations on the cessation of feeding with accurate information on the condition of the reproductive organs.

The observations on haddock of the western Atlantic lead to conclusions opposite to those enunciated by Russell. Bigelow and Welsh (1924) made an

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observation at Cape Ann that "the haddock fast even more rigorously than cod at spawning time, because more than ninety-five percent of the hundreds of fish caught in the gill nets were totally empty, and because line trawls set nearby were bringing in very few haddock but were taking hake in fair numbers". Vladykov (1934) observed that haddock with running sexual products were taken in gill nets ("cod nets") at Peggy's Cove, N.S., when practically no haddock were caught with hook and line on the same grounds, and in 1935 he saw large quantities of haddock caught in haddock traps at Petit de Grat and Ingonish, N.S., whereas catches of this fish on hook and line were extremely small. The majority of these fish were in stage 3 of maturity (see below). One of the authors (Homans) examined 449 spawning haddock taken in mackerel traps at French Village, N.S., in late May, 1935. Only four fish had food in their stomachs and intestines. All these fish had been in the traps only a few hours. McKenzie (1940) in a study of spawning haddock at Jordan Harbour, N.S., observed that "so little do these fish feed that line trawls set all around the trap [haddock trap net] often yield not one haddock, while thousands of pounds are taken in the trap".

In order to shed more light on this problem an investigation was carried on during 1934–35. During the period from September, 1934, to August, 1935, a large number of haddock were examined and data collected on the proportions of haddock feeding at different months of the year, the amount of food taken and the proportions in the various sexual stages.

TABLE I. Definitions of the sexual stages for haddock.

Stage	Female	Male
1	Ovaries small and firm. Contents reddish yellow and bright looking. Membrane thin and somewhat transparent.	Small testes appear as a clear, crimped and slender string; colourless to gray.
2	Ovaries slightly larger than in 1, but still small and firm. Contents microscopic, yellow, opaque eggs. Membrane thin.	Testes grow gradually in size. Pinkish or flesh coloured, wavy and slightly distended.
3	Ovaries larger and becoming reddish with numerous blood vessels. The minute opaque eggs are now visible to the naked eye and give the ovaries a granular appearance.	The testes are beginning to turn white, are wavy, somewhat larger and distended, with fine, rather conspicuous blood vessels. No milt runs when pressure is applied.
4	Ovaries well developed, reddish golden in colour, and opaque with blood vessels becoming inconspicuous. Contents consist of some translucent eggs, and eggs which are yellow and opaque. Few eggs running.	The testes are distinctly wavy, white and quite distended, large lobes. Only few drops sperm obtained by pressing.
5	Ovaries very much developed. Eggs transparent or light amber colour and running freely.	The testes are very white and fully distended. Milt runs freely at the slightest pressure.
6	Ovaries soft, flabby and bloody. Practically no eggs remain. Membrane thick and tough.	The testes are shrunken. Very large vas deferens. Later become wrinkled and string-like.

MATERIALS AND METHODS

The present report is based on the examination of the stomachs and gonads of some five thousand haddock taken on the Nova Scotian offshore banks. The haddock were captured by steam trawlers fishing in waters not deeper than 70 fathoms.

The mass of food in the stomachs was weighed and the percentage of stomachs with food was recorder for each sample. In order to facilitate comparison between fish in different stages of maturity they are generally classified into several groups according to the degree of ripening. Unfortunately, there is no standard system in general use. A review of different methods of classifying maturity stages, mainly for clupeids, is given by Kisselevitch (1923). In the present paper data on the sexual stages were recorded by means of a system whereby the full sexual cycle for both sexes was divided into six stages. This system is based on the original description of an eight-stage system applicable to all species of marine fishes, proposed by Maier (1906) and on the system used by Raitt (1933). A good deal of modification has been made in combining them and adapting them especially to haddock. Table I gives a description of the six stages for both male and female haddock.

RESULTS

Proportions of Haddock Feeding at Various Seasons

The number of stomachs which contained food and the number which were empty was determined for each sample examined. The results have been converted to percentages and are shown in Figure I. For this purpose the samples

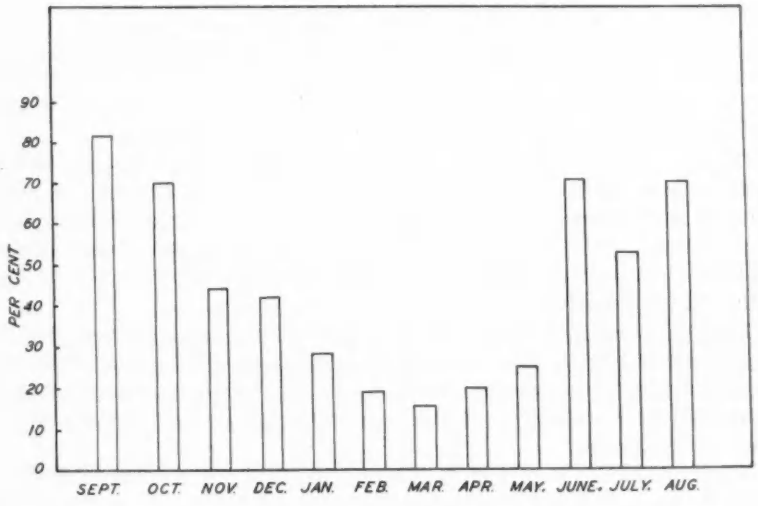

Figure 1. Monthly variation in the numbers of feeding haddock, expressed in percentages of monthly samples.

have been grouped and recorded for each month. The minimum number of stomachs examined in any one month was 260.

It is seen that the proportion of haddock with food in their stomachs diminished markedly from September to March. Thus, in September, it was about 80% and in March only 16%. April and May saw a slight increase and there was a pronounced increase in June when about 72% of those examined had food in their stomachs. In July a decrease to 52% coincided with abnormally high water temperatures on the banks at that time varying from 8.5° to 11°C. (Vladykov, 1934). There can be little doubt that the extremely warm water was mainly responsible for the decrease. After July the number of haddock taking food increased, amounting to 70% in August.

No significant differences in the rates of feeding were observed between the sexes. Males and females were apparently equally affected by the events leading up to and including spawning.

The period from September, 1934, to August, 1935, may be divided into two parts from the point of view of the proportion of haddock feeding. A *summer and fall feeding season* (June to October) is characterized by a relatively high percentage of feeding haddock, varying from 70% to 80%. This is followed by a *winter and spring season* (November to May) during which time a large proportion of haddock (from 50% to 85%) do not take food. Only a very small percentage of haddock continue to feed in the spring months (February to May). During this period, which may be called the *spawning period*, haddock belonging to these schools are spawning. Following the spawning act a large percentage of the spent haddock resume feeding, regaining the weight lost through the spawning.

Variations in the Amounts of Food Taken

The weight of food found in each stomach was recorded in grams. Figure 2 shows the average weight of food, in those haddock stomachs which contained any, for each month of the period under consideration. The average weight of haddock remained very nearly the same throughout the period.

It is seen that in September the mean weight of food per stomach was about 10 g. Month by month this figure gradually dropped to a low of 1.5 g. in February. It then gradually increased and by June was 7 g. per stomach. In July feed are less abundant in late winter, when feeding is least, than in summer, there was a tremendous increase, the average per stomach being 26 g. In August it dropped sharply to 7 g.

The above values for the average weight of food eaten per haddock strike one as being extremely low. However, it is to be understood that these values represent the weight of food found in the stomach alone, no record being kept of the food in the intestines, which normally equals that in the stomach and sometimes exceeds it.

Figure 2 shows a very definite seasonal change in the quantity of food taken by the haddock. This change is not believed to be dependent on the available food supply, because there is no evidence that the animals on which the haddock

when feeding is heaviest (Vladykov and Homans, MS). Furthermore, temperatures where haddock were found varied between 4°C. and 8°C. from October to June, and are thus considered to be quite favourable for haddock feeding (Vladykov, 1934).

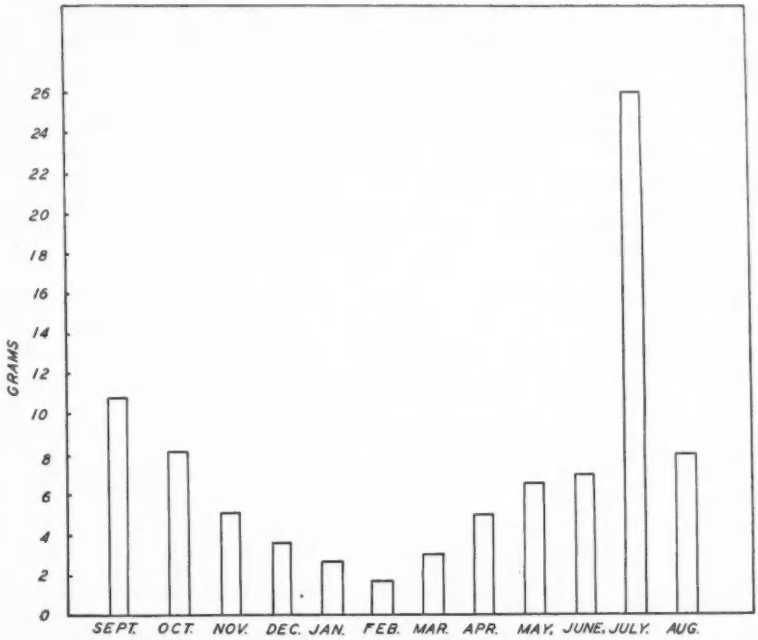

FIGURE 2. Monthly variation in the average amount of food taken by feeding haddock expressed as grams per stomach.

It is a well-known fact that certain fishes usually disgorge the whole of their stomach contents when caught. Bull (1928) states that the whiting (*Gadus merlangus*) usually does so. The authors have observed the same phenomenon taking place with squirrel hake (*Urophycis chuss*) and silver hake (*Merluccius bilinearis*), but rarely in the case of haddock caught either by hook and line or with otter trawl. Hickling (1927) found that in water shallower than 50 fathoms less than 2% of hake disgorged the stomach contents when caught, whereas at depths of 120 fathoms about 50% did so. As the great majority of the haddock examined were caught in depths of from 40 to 50 fathoms, and as haddock are not nearly as susceptible to disgorging of stomach contents as hake, this factor has been considered insignificant.

CORRELATION OF FEEDING WITH THE SEXUAL CYCLE

In view of the earlier observations on the feeding habits of haddock in relation to the spawning period, an attempt has been made to correlate the number

of feeding fish, and the amount of food taken per fish, with the spawning cycle. The degree of sexual development was recorded using the six-stage system described in Table I. These data have been summarized in Figure 3.

For purposes of brevity and convenience, stages 1 and 2 have been grouped together and have been called the "recovery period". This is the period in which the haddock recover from the spent condition and make ready for the important changes which precede the next spawning act. Stages 3 and 4 have also been grouped and designated as the "ripening period". This phase follows the recovery period and is characterized by the marked changes which the gonads undergo in preparation for spawning. Stage 5 is the actual spawning stage when the eggs and milt are flowing freely, or flow freely when pressure is applied to the gonads. Stage 6 is used to describe the spent haddock.

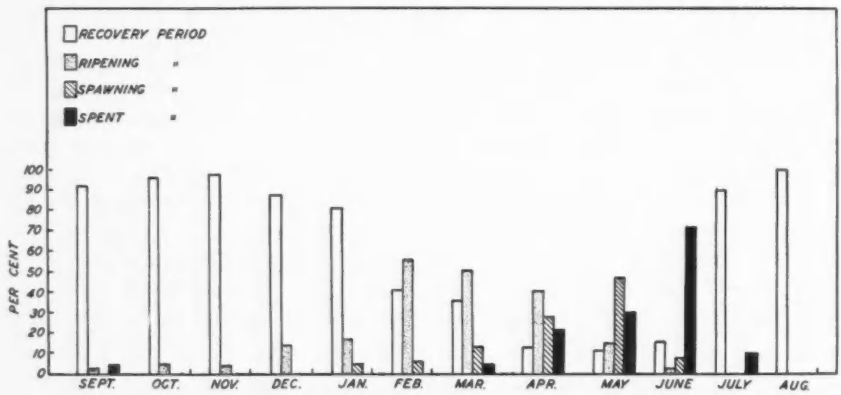

FIGURE 3. Number of haddock for each sexual period given as percentages of each month's samples.

It is seen from Figure 3 that during the period July to January the great majority of the haddock on the Western Banks were in the recovery period. In December and January the first significant indications of ripening haddock appeared. Most of the haddock passed into the ripening period very quickly, for by the end of February most of those examined were in early and advanced degrees of ripening and a small number had commenced to spawn. During March and April considerable numbers of haddock spawned and the proportion of spent fish increased. By the end of June all spawning was practically over, as indicated by the large numbers of spent fish.

It has been shown that during the spring months (February to May) less than 25% of all haddock examined had food in their stomachs, whereas for the remainder of the year as many as 82% of the haddock examined were feeding. It is also during the spring months that the least amount of food is eaten. In addition to the above, it has been shown that in the spring months (February to May) the haddock from offshore banks ripen and spawn.

The facts advanced make it reasonably certain that most haddock cease to take food during the ripening period. Observations made on substantial numbers of haddock sampled from individual hauls showed that those which were in the less advanced stages of maturity (stages 1 to 3) and in the spent condition had been feeding, but that those in the advanced stages (stages 4 and 5) had not been feeding. These haddock continue to fast throughout the spawning period. Following the completion of spawning, large numbers of haddock commence to take food, but a short period passes while they are in the spent condition, before they regain their appetites for very heavy feeding. Once the full appetite has been regained, voracious feeding is carried on for a time. This spurt of heavy feeding enables the spent haddock to regain lost weight.

It is concluded that changes in the life cycle of the haddock affect its feeding habits, since the variations in the number of feeding haddock at different times of the year can be correlated with the changes in the ripening cycle. There is, of course, always a chance that a certain number of haddock, regardless of the stage of maturity, may cease to take food. This cessation may be due to various diseases, parasites, etc., or to a sharp change in water temperature. However, the number of haddock affected by these causes plays a very small role in the annual fast of haddock during the late winter and spring months.

Correlation of Feeding with Catches on Hook and Line

Table II shows a comparison between catches of haddock made by steam trawlers using otter trawls and those made by fishing schooners with hook and line, and reveals some interesting facts. Actual observations made from fishing schooners during the period 1934–35 showed that during December, 1934, slightly more than 22 lb. of haddock (gutted weight) were taken per line (50 hooks). This figure dropped each succeeding month, until by March the catch was less than 7 lb. per line and in April it was only 9 lb. The very small catches of haddock made by schooners using lines during February to April, 1935, on offshore banks were due to the advanced ripening of these fish and not to a decrease in the number of fish on the fishing grounds as is clearly indicated by the increase

Table II. Comparison of haddock catches made by schooners and trawlers on the Western Banks during the winter and spring of 1934–35.

Month	Schooner catch		Trawler catch	
	Number of trips	Catch per line	Number of days fishing	Catch per day
		lb.		*lb.*
November, 1934	11	8	9½	5,052
December	5	22	16½	7,091
January, 1935	7	16	19½	11,436
February	4	9	18½	20,810
March	15	7	19½	22,872
April	7	9	18	18,555

in the catch per day made by steam trawlers from November, 1934, to April, 1935. In November their catch was about 5,000 lb. per day; by March it had risen to nearly 23,000 lb. and in April was still well over 18,000 lb.

In conclusion, it may be stated that a close relationship exists between the sexual cycle of the haddock, its feeding habits and the quantity obtained in commercial fishing. As is well known, fish congregate on the spawning grounds in large numbers prior to and during the spawning period. This enables trawlers to make large catches as indicated by the increase in catch per haul during the spawning season of 1935. On the other hand, the hook and line catches on the same grounds dropped during this period because of the cessation of feeding on the part of most of the large haddock as spawning time approached. Good catches of large haddock may be obtained with hook and line during the spawning season only when they are in the less advanced ripening stages or after spawning. When these fish reach maturity stage 4 they almost all cease to take bait.

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New Stoneflies (Plecoptera) from Western North America[1]

By Stanley G. Jewett, Jr.[2]

ABSTRACT

Descriptions are presented of the new species *Capnia cygna, C. petila, C. porrecta, C. sextuberculata* and *Isoperla rainiera.* For seven already-named species, previously unknown male or female adults or nymphs are described.

Western North America is richly endowed with aquatic insects, and stoneflies constitute an important element in this fauna. In studying a considerable amount of material from the area, a number of poorly known and new species have been encountered. Twelve of these, of which five are new, are treated below. For providing specimens upon which a part of this paper is based I am indebted to Dr. Maurice T. James, Department of Zoology, State College of Washington, Pullman, Washington; Dr. W. F. Barr, Entomology Department, University of Idaho, Moscow, Idaho; Dr. D. G. Denning, Velsicol Corporation, Berkeley, California; and to Mr. James H. Baker, Baker, Oregon.

Nemoura (Malenka) tina Ricker

1952. *Nemoura (Malenka) tina* Ricker, Syst. Studies Plecop., p. 35, male.

Female: Length to wing tips: 9 mm. Length of body: 7.5 mm. Similar to the male in general morphological details, slightly larger in size. The 8th sternite is completely bisected by a notch which is margined by heavy sclerotization in its narrow anterior third, Figure 1.

Allotype female: Rock Creek Ranger Station, Magic Mt., 6,400–6,700 feet elevation, Twin Falls County, Idaho, July 20, 1952, Borys Malkin and W. F. Barr. Deposited in the collection of the California Academy of Sciences. Five males and nine additional females were taken with the allotype.

The female of this species is apparently indistinguishable from that of *N. biloba* Claassen, known only from southern California.

Megaleuctra kincaidi Frison

1942. *Megaleuctra kincaidi* Frison, Pan-Pac. Ent. **18**(1): 15–16, male.

Nymph: A mature male nymph collected by W. F. Barr on April 25, 1953, at Moscow Mt., Latah County, Idaho, is described as follows: Length of body: 15 mm. Cercal segments at least 17, of antennae over 40 (tips missing). Gills absent. General colour light brown. Body elongated, the wing pads extending nearly parallel to the axis of the body, Figure 2. Body covered with fine hairs in length equal to one-fifth the length of the middle abdominal segments. A ring

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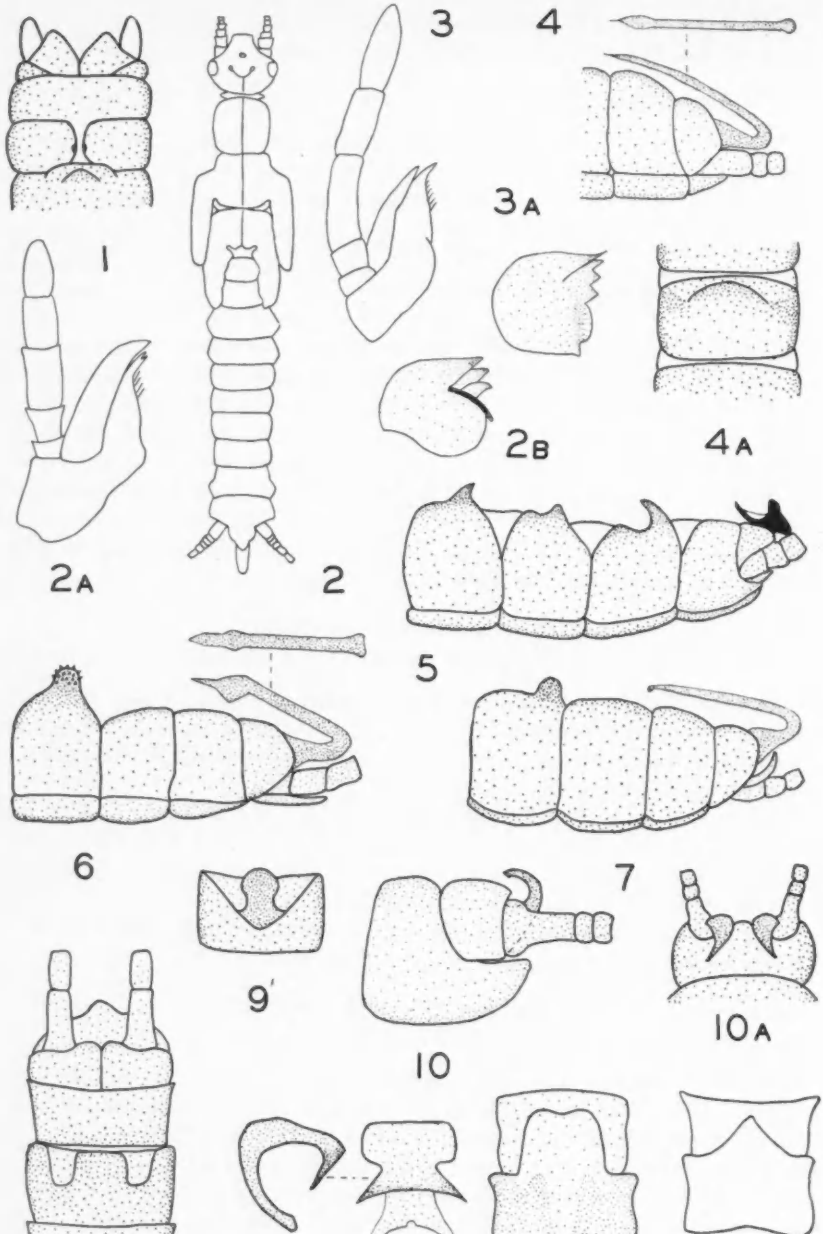
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of spines around the posterior end of the cercal segments, coarse stiff hairs or bristles on legs, particularly on outer surfaces; bristles absent elsewhere. A pair of prominent spurs at the inner distal end of all the tibiae. A continuous membranous fold present along the sides of the first 7 abdominal segments. Tenth sternite drawn out, its tip upturned, enclosing the bulbous-tipped, recurved ventral process. Tenth tergite drawn out and containing a dorsal sclerotized structure. Subanal lobes bulbous, not fused distally, rather hidden between the 10th tergite and 10th sternite.

Galea exceeding lacinia, the lacinia with an inner spine and a comb of fine hairs, Figure 2A. Right mandible, Figure 2B, with 3 large, heavy teeth and a heavily sclerotized plate behind them.

Since specimens of *Megaleuctra* are rarely collected, the following record of an adult male specimen of *M. kincaidi* is presented: Bell Creek, tributary of Lake Cle Elum, Kititas County, Washington, May 22, 1946, S. G. Jewett, Jr.

Perlomyia collaris Banks

1906. *Perlomyia collaris* Banks, Can. Ent. **38**: 338, female.
1936. *Perlomyia solitaria* Frison, Ann. Ent. Soc. Amer., **29**: 261, male.
1936. *Perlomyia sobrina* Frison, ibid., **29**: 262, female.
1943. *Perlomyia collaris* Ricker, Stoneflies SW B.C., p. 82, established synonymy.

NYMPH: Several exuviae were collected by the writer with a series of adults of this species on March 14, 1953, along the Necanicum River, Clatsop County, Oregon. From these, the following characterization of the nymph can be made: Length of body: about 12 mm. Cercal segments at least 23, of antennae about 100. Gills absent. Body elongated, the wing pads only very slightly angled from the axis of the body. Body covered with extremely fine pile, appearing almost naked. The subanal lobes are fused mesally for about half their length leaving a notch at the tip. Stout hairs (hardly bristles) on the legs and as a ring around each cercal segment. A pair of spurs present on the inner distal end of the tibiae. A continuous membranous fold extends along the sides of the first 7 abdominal segments.

Galea not quite reaching the end of the lacinia; the latter has an inner spine (parallel with the outer spine in side view) and a comb of hairs on the inner surface, Figure 3. Right mandible, Figure 3A, has an irregular row of 4 teeth and behind them a heavily sclerotized plate with a rounded surface.

FIGURES 1–12

1, *Nemoura* (*Malenka*) *tina*, terminal sternites of female allotype. **2,** *Megaleuctra kincaidi*, outline of male nymph; **2A,** right maxilla of nymph; **2B,** right mandible of nymph. **3,** *Perlomyia collaris*, right maxilla of nymph; **3A,** right mandible of nymph. **4,** *Capnia porrecta*, male genitalia, lateral aspect; **4A,** 8th sternite of female. **5,** *Capnia sextuberculata*, male genitalia, lateral aspect. **6,** *Capnia cygna*, male genitalia, lateral aspect. **7,** *Capnia petila*, male genitalia, lateral spect. **8,** *Isocapnia abbreviata*, terminal sternites of female allotype. **9,** *Isoperla rainiera*, ventral lobe on male 8th sternite; **9A,** aedeagal structure in lateral view and from above. **10,** *Isoperla phalerata*, male genitalia, lateral aspect; **10A,** male genitalia from above. **11,** *Isoperla gravitans*, 8th sternite of female allotype. **12,** *Alloperla delicata*, 8th sternite of female allotype.

Capnia cygna Jewett, new species

MALE: Length to tip of wings: 4 mm. Length of body: 7.5 mm. In general features similar to other species of the genus; wings short. This new species differs from other described species of the genus *Capnia* in the following combination of characters: A prominent median tubercle on the surface of which are many short, thick spines, present on the rear margin of the 7th tergite. Tenth tergite divided by a median membranous area which extends across tergites 9 and 8, the anterior borders of which have a transverse band so that they are not completely divided. A recurved supra-anal process extending nearly across the 9th tergite expands distally in lateral view, then contracts to a cylindrical point to form a tip which suggests the shape of a bird's head, Figure 6.

Holotype male and paratype male: no data. A mature male nymph of the same species is labelled "Rock Lake, Haugen, 4/11/36" and was probably taken from a tributary of Rock Lake, Whitman County, Washington. Holotype deposited in the collection of the State College of Washington, the paratype in the collection of the California Academy of Sciences, the mature nymph (with 2 female nymphs of *Capnia*) in the writer's collection.

The shape of the supra-anal process together with the spinous knob on the 7th tergite distinguish this species from previously described members of the genus.

Capnia petila Jewett, new species

MALE: Length to tip of wings: 6 mm. Length of body: 5.5 mm. Similar in general morphological details to other members of the genus; wings of normal length. No special structures on first 6 tergites; a prominent median tubercle on the 7th tergite. Tenth tergite divided by a median membranous area. Tergites 9 and 8 without membranous areas. A recurved, slender, cylindrical supra-anal process extending to the rear margin of the 8th tergite is bluntly tipped, the tip bent very slightly downward, Figure 7.

Holotype male and paratype male: Spring Creek, tributary to Powder River, Baker County, Oregon, March 30, 1952, J. H. Baker. Two additional paratypes were taken at the same locality by the same collector on March 23, 1952. Holotype deposited in the collection of the California Academy of Sciences, paratypes in the collections of the writer, Wm. E. Ricker, and the Illinois Natural History Survey.

Among described species of *Capnia*, this new species most closely resembles *C. wanica* Frison, but it differs from that species most noticeably in having a supra-anal process, the reflexed portion of which is nearly straight whereas in *C. wanica* this is strongly curved throughout its length.

Capnia porrecta Jewett, new species

Length to wing tips: male 8 mm.; female 9 mm. Length of body: male 6 mm.; female 6.5 mm.

MALE: This species closely resembles *C. projecta* Frison in size, wing markings, and in lacking tubercles on the abdominal tergites. It differs in having a more slender supra-anal process with the tip of the process extending almost

medially (side view) instead of ventrally as in *C. projecta*, Figure 4. In *C. projecta* the width of the supra-anal process in dorsal view is about one-sixth the length, exclusive of the terminal sharp tip, and in this new species it is about one-tenth the length, exclusive of the terminal tip.

FEMALE: Similar in general morphological details to the male. The subgenital plate, Figure 4A, terminates in a broadly rounded central portion which is bordered on either side by an almost membranous area.

Holotype male, allotype female, and 23 male and 16 female paratypes: Santiam River near Jefferson, Linn County, Oregon, October 21, 1948, S. G. Jewett, Jr. Additional paratypes from near the mouth of Clackamas River, Clackamas County, Oregon, collected by the writer, as follows: October 21, 1948, 1 male; October 31, 1948, 7 males; November 27, 1949, 1 male; December 26, 1949, 1 male. Holo- and allotypes deposited in the collection of the California Academy of Sciences. Paratypes deposited in the collections of the writer, Wm. E. Ricker, Illinois Natural History Survey, California Academy of Sciences, and Cornell University.

From most described species of *Capnia* this new species differs in the banded wing pattern; from *C. projecta* the male differs in the median position (side view) of the terminal spine on the supra-anal process and in the length to width ratio of the supra-anal process. The female cannot be separated with assurance from several other described species except for the wing colour pattern which is similar only to *C. projecta*. The subgenital plate resembles that of some specimens of *C. projecta*.

This species emerges with *C. projecta*, and the peak of emergence of the two probably coincides. It has been collected only from large streams whereas *C. projecta* occurs commonly in small streams as well as large ones.

Capnia sextuberculata Jewett, new species

MALE: Length to tip of wings: 4 mm. Length of body: 6 mm. In general morphological details similar to other species of the genus; wings short. The male is quite unlike that of previously described species of the genus and may be characterized briefly as follows: Abdominal tergites 1 through 5 without special features; tergite 6 with a pair of raised, conical tubercles located on the posterior half of the tergite, the tips of which are directed backwards; tergite 7 with a pair of raised tubercles located slightly behind the middle of the tergite; tergite 8 with a pair of raised, forward-directed, hook-like tubercles near the rear margin of the tergite, Figure 5. Membranous areas occur on tergites 6 to 9. Tergite 10 nearly bisected by a membranous median portion on which rests the short, recurved supra-anal process. This structure consists of an upturned, ribbon-like portion which extends forward across the posterior quarter of the 9th tergite and which is membranous dorsally, heavily sclerotized ventrally, and a heavily sclerotized portion the base of which extends, in side view, both dorsad and ventrad from the distal end of the 10th tergite, Figure 5.

Holotype male and 3 male paratypes: Spring Creek, tributary of Powder River, Baker County, Oregon, March 23, 1952, J. H. Baker. An additional male paratype from the same locality and taken by the same collector is dated April,

1952. Holotype deposited in the collection of the California Academy of Sciences. Paratypes deposited in the collection of the writer, Wm. E. Ricker, and the Illinois Natural History Survey.

Isocapnia abbreviata Frison

1942. *Isocapnia abbreviata* Frison, Pan-Pac. Ent. **18**: 71–72, male.

FEMALE: Length to wing tips: 11 mm. Length of body: 8.5 mm. In general features similar to the male but slightly larger in size. Eighth abdominal sternite with nearly rectangular membranous areas on either side of a central sclerotized portion, the areas extending from about the middle of the sternite to the posterior border, Figure 8. The incised membranous areas may be almost wholly sclerotized in old, mature specimens and thus not discernible. One such specimen taken with the allotype has a subgenital plate suggestive of that illustrated for *Isocapnia integra* Hanson (*Bull. Brooklyn Ent. Soc.* **38**(5): 161, fig. 6, 1943).

Allotype female: Mouth of Rogue River, Curry County, Oregon, March 30, 1949, S. G. Jewett, Jr. Deposited in the collection of the California Academy of Sciences. Three male and four additional female specimens were taken with the allotype.

The small size and distinctive subgenital plate (at least in teneral specimens) readily separate the female of *I. abbreviata* from females of other described species of the genus.

Isoperla gravitans (Needham and Claassen)

1925. *Clioperla gravitans* Needham and Claassen, Monog. Plecop., pp. 138–139, male.

FEMALE: Length to tip of wings: 20 mm. Length of body: 15 mm. Similar in general morphological details to the male but somewhat larger in size. The subgenital plate, Figure 11, is produced over two-thirds to three-fourths of the 9th sternite, and its broadly rounded tip is slightly emarginate. Distally the plate is yellow in the allotype, the yellow area invading the brown colour of the base medially as a V to the base of the segment. Another female specimen is somewhat teneral and lacks the striking yellow colouring of the allotype.

Allotype female: Youngs River, Clatsop County, Oregon, May 1, 1940, S. G. Jewett, Jr. Deposited in the collection of the California Academy of Sciences.

Since this species has been recorded previously only from Olympia, Washington, the following records are presented: Spring near Ellsworth, Clark County, Washington, S. G. Jewett, Jr.: March 27, 1941, 1 female; April 1, 1941, 1 male; April 14, 1941, 2 males; Big Creek, Clatsop County, Oregon, May 9, 1947, S. G. Jewett, Jr., 1 male.

Isoperla phalerata (Needham)

1917. *Dictyogenus* (?) *phaleratus* Needham, in Smith, Trans. Am. Ent. Soc., **43**: 485, female.
1925. *Perla phalerata* Needham and Claassen, Monog. Plecop., p. 91, female.
1952. *Isogenus phaleratus* Ricker, Syst. Studies Plecop., p. 131. Suggests species may belong to *Isoperla*.

MALE: Length to tip of wings: 13 mm. Length of body: 11 mm. In general features similar to the female with variable crossveins between the branches of the radial sector. Head pattern similar to that of the holotype as illustrated by Ricker (*ibid.*, p. 130, fig. 82), but in some specimens there is a light brown pig-

mented area behind the rear ocelli. The subanal lobes, Figures 10 and 10A, broad basally, tapered to blunt tips, the inner marginal surfaces of the tips flattened as in *I. pinta* Frison. The 9th sternite is long with the distal end curled inward. The aedeagus is without major sclerotization. The lobe on the 8th sternite is rather inconspicuous, wider than long.

Allotype male: Grande Ronde River, La Grande, Union County, Oregon, June 6, 1948, D. G. Denning. Deposited in the collection of the California Academy of Sciences.

Additional records of this species are as follows: "Colo.", 1 female; Woods Landing, Laramie River, Wyoming, June 28, 1948, D. G. Denning, 1 male; Trout Creek, Harney County, Oregon, May 23, 1950, Fender and Jewett, 1 male (brachypterous), 2 females.

This species is readily separated from other members of the genus by the crossveins in the wings and by the head pattern. It might be noted that in the female specimens which I have examined the tip of the subgenital plate is shallowly emarginate, not broadly rounded as in Ricker's illustration of the holotype (*ibid.*, p. 130, fig. 84).

Isoperla rainiera Jewett, new species

MALE: Length to tip of wings: 10 mm. Length of body: 9 mm. In general features this species bears close similarity to *I. fusca* Needham and Claassen. Head mostly dark with lighter areas in the ocellar triangle and at the outer corners of the rear of the head. Subanal lobes recurved, the tips sharp, sclerotized on outer surfaces, membranous on inner faces, very similar to those of *I. fusca*. Lobe on the 8th sternite pedicellate, rounded distally, Figure 9. A sclerotized process in the aedeagus has the distal end very broadly emarginate and turned downward very sharply, each outer corner terminating in a broad, sharp tip, the base also emarginate, the corner tips of which are rounded, Figure 9A.

Holotype male: Mount Ranier National Park, August 10, 1941, Lipovsky. Deposited in the collection of the State College of Washington.

This species differs from other described members of the genus principally in the shape of the sclerotized process of the aedeagus.

Alloperla (*Alloperla*) *delicata* Frison

1935. *Alloperla delicata* Frison, Trans. Am. Ent. Soc., **61**: 334, male.

FEMALE: Length to tip of wings: 11 mm. Length of body: 9 mm. The subgenital plate, Figure 12, is triangularly produced and has a narrowly rounded tip.

Allotype female: Eagle Creek, Clackamas County, Oregon, June 27, 1948, S. G. Jewett, Jr. Deposited in the collection of the California Academy of Sciences. Forty-four males and 12 additional females were taken with the allotype.

The shape of the subgenital plate distinguishes this species from other members of the subgenus found within the known range of *A. delicata*.

Unlike other western North American species of the subgenus described to date, *A. delicata* may be yellow in life as well as the usual green. The series from which the allotype was selected ranged in colour from bright green to deep lemon yellow before preservation in alcohol.

Movements of Cutthroat Trout after Different Periods of Retention Upstream and Downstream from their Homes[1]

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ABSTRACT

A homing experiment of cutthroat trout (*Salmo clarki*) was carried out in Gorge Creek, a small trout stream more or less typical of the streams of the eastern slopes of the Rocky Mountains in Alberta. A half-mile portion of the stream was screened off and, into the enclosure thus formed, 105 trout were transferred from above and 104 from below. Each of these was given a numbered tag and the home locality was recorded. The transfers were made from June 24 to August 13. On August 15 the screens were removed; from September 3 to 5 most of the experimental area was poisoned with Fish Tox and the localities of tagged fish recorded. It was found that most of the trout that had been confined for 30 or more days remained in the enclosure area, i.e., they had adjusted to new homes. The exceptions appear to be the result of random movements. Trout of upstream origin, confined for less than 30 days, move toward their original home territory. Trout of downstream origin, confined for less than 30 days, show very much less ability to move toward or to find their homes. The hypothesis is put forward that trout are guided by smell in finding home.

A few observations on size of home territory suggest that it is small, perhaps not more than 20 yards of stream. Trout may inhabit the same area of stream for at least three years.

INTRODUCTION

The behaviour of fishes living in inland streams has been very little studied. Most of the information available on home territories and territorial behaviour of stream fishes comes from observations made during the course of researches on other aspects of stream ecology. Gerking (1953) has reviewed the literature on the evidence of territorial behaviour in stream fishes. He found several references to stream fish occupying the same area of a stream for long periods of time, if not for life. Evidently very little has been done toward establishing the sizes of the home territories occupied by fish, or their ability to return to them if involuntarily moved away. Dr. Gerking conducted experiments on two streams in Indiana which reveal very definite and restricted home territories for longear sunfish, rock bass and green sunfish, and a somewhat larger, but still very definite home territory for larger bass and suckers. In one series of experiments he transplanted longear sunfish and rock bass from one pool upstream, over a riffle, to a second pool. Within two weeks the fish had returned to their home pool. Although Gerking admits that this might be a simple homing reaction, he favours the interpretation that territorial behaviour (i.e., aggressive action) of the original inhabitants of the pool forced the newcomers out.

Recently Allen (1951) has shown that brown trout occupy very definite home territories in a stream.

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During the course of experiments on the survival of cutthroat trout (*Salmo clarki*) in Gorge Creek, casual observations on home territories and homing behaviour were made. In the period July 5–31, 1951, 152 wild cutthroat trout, ranging from 1 to 7 ounces (average, 2.6 ounces, 73 grams) were caught by angling, given numbered Petersen tags and transferred downstream to an enclosure one-half mile in length where they were retained for 69 days. The first response to this change of locale was a very determined assault on the upstream screen of the enclosure. An undetermined number managed to get through the screen; some of these were later recaptured in what memory suggested were the same pools from which they were first taken. As no records had been kept this could not be proven. The struggle to return upstream was so strong that 25 trout killed themselves by beating against the screen. This occurred in late July, long past spawning time, so that spawning urges did not motivate the trout. The only explanation was that the fish were attempting to return home. The fact that none of the fish attempted to pass through the screen at the downstream end of the enclosure lends strength to the hypothesis; i.e., all the trout had been transferred from upstream.

Of the original 152 fish, it is believed that 127 remained in the enclosure for 69 days. The screens were then removed and the fish were free to roam. Nevertheless, next summer (1952), 59 of these trout were found in the area where they had been enclosed the previous year. Two years later (1953) 37 were found still inhabiting the enclosure area. Annual mortality rates in Gorge Creek, where these observations were made, have been estimated from marking experiments at approximately 60 per cent. Thus 127 fish should be reduced to 51 in one year and 20 in two years; 59 and 37 were actually found. There seems little doubt, therefore, that, after having been forced to remain in one area for 69 days, the trout accepted it as home and lost their desire to return to their original place of capture.

These more or less casual observations suggest two things: first that the trout have a home area to which they will return when removed from it, and second, that the forced occupation of a new area for 69 days leads to loss of the urge to return to home—the new area has become home.

In 1953 an experiment was carried out at Gorge Creek to determine if displaced fish would actually move toward home and, if so, how long this tendency to home would persist in fish forcibly restrained from returning home.

DESCRIPTION OF GORGE CREEK AND THE EXPERIMENTAL AREA

Gorge Creek is a small tributary of the Sheep River of the South Saskatchewan River system. It flows into the Sheep at an elevation of 4,800 feet, some 20 miles west of the town of Turner Valley, Alberta. It is a fairly typical east slope trout stream, 15 to 30 feet wide, with shale banks, rocky pools and gravelly riffles. The stretch of the stream used in the homing experiment consists of approximately 4,000 yards flowing through a winding, steep-walled canyon. The gradient in this stretch is 22 feet per mile, all a gradual descent. No obstructions to free movement of trout up or down exist, except that in late summer, one

partial obstruction developed during a low-water period. The speed of the current varies from 7.0 miles per hour in May to 1.5 miles per hour in September. During the period of the experiment the rate of flow was from 1.5–2.0 miles per hour.

Maximum and minimum daily temperatures have been recorded for four summers. No linear temperature gradient was found in the experimental area. The daily temperature change amounted to 14°–16°F.

Tagging and recovery experiments in 1947, 1948 and 1950–52 showed a resident population of cutthroat trout of approximately 800 per mile. Poisoning in 1953 gave an actual count of 722 trout resident in 1,225 yards of the experimental area which is 1,000 per mile. These trout range from 1 to 7 ounces (average, 3.0 ounces, 85 grams) and are a mature, breeding population, up to five years old.

Earlier work on the stream has established that these trout are non-migratory; thus, in 1948, a two-way trap was operated from shortly after break-up in April until after freeze-up in November. No significant movement into or out of the creek was found. Fish fin-clipped in 1947 were recovered in 1948 and fish tagged in 1951 were recovered in 1952 and 1953. During the summer there can be very little movement within the creek itself; wire screens across the creek in three places (two summers) and four places (one summer) demonstrate this. Such screens were used to retain tagged hatchery fish in enclosures; in attempts to escape these fish often stuck in the screens. No untagged fish were found wedged in the screens. Observations of spawning behaviour have also shown that these trout spawn along the whole length of the stream; i.e., there is no movement up or down to spawning areas.

The stream has been, since 1950, the site of the main activities of the Alberta Biological Station, which is operated jointly by the University of Alberta and the Alberta Department of Lands and Forests.

DESIGN OF THE EXPERIMENT

During the period June 18 to June 22, two fish-tight screens were installed in Gorge Creek so as to create an enclosure one-half mile long. The pools in the stream above the enclosure were numbered and marked from 1 to 33; the series extended to 2,090 yards above the enclosure. The pools below the enclosure were lettered from A to O and extended to 750 yards below the enclosure.

From June 24 to August 13, cutthroat trout were caught by angling from these numbered and lettered pools. Each trout was given a numbered Petersen tag, weighed to the nearest quarter ounce, and then released in the enclosure. A record was made of the tag number, weight, pool letter or number and date. In this way 209 were transferred to the enclosure, 105 from above and 104 from below. The fish varied in weight from 1¼ to 12 ounces. The upstream group had an average weight of 3.3 ounces (94 grams), the downstream group of 3.0 ounces (85 grams).

As the transfers were spread fairly evenly over the whole period June 24 to August 13, by August 15 the enclosure contained fish with periods of confinement

varying from 2 days to 52 days. On this day, August 15, the screens were removed and the fish were free to move up or down. In this way it was expected that any differences in behaviour induced by variable lengths of confinement could be identified.

A preliminary hypothesis was that the fish would find their way home upstream by sense of smell; if fish could also "home" downstream, smell would, of course, be ruled out. To gain some information on this point, half of the fish involved in the experiment had their nares plugged with batting (an idea borrowed from Dr. A. D. Hasler). However, the fish rubbed the cotton out within a few days and the results show no differences in behaviour between "plugged" and normal trout.

From August 16 to September 3 fishing was carried out to determine the locations of tagged fish. A total of 91 records was obtained in this way. From September 3 to 5 the stream was poisoned with Fish Tox and 141 tagged trout were recovered. The poisoning was done over short stretches, beginning downstream; thus the location of tagged fish killed could be accurately known. The trout had been free to move for from 19 to 21 days.

The combined returns from angling and poisoning provided data for analysis as follows:

Total number tagged and transferred from upstream		105
Number of records obtained	94	
Died in enclosure	1	
Data confused in field book	2	
No record	8	
Total number tagged and transferred from downstream		104
Number of records obtained	87	
Died in enclosure	1	
No record	16	

SOURCES OF ERROR

There is a possibility that some of the fish, tagged in June, were not at home. This is particularly true of downstream fish which may have been downstream because of high water earlier in the month. Five fish, tagged below the enclosure, were found later to have made their way through the upper screen and taken up residence in the upper part of Gorge Creek. One of these fish moved 3,245 yards, another 2,670 yards, and a third 2,155 yards. These distances are so great in comparison to movements of the other trout that it is highly probably that they were away from home when first caught. However, since this is merely supposition, these five fish, and other doubtful records, have all been included in the analyses.

Another source of error is the failure to poison the area from Pool 18 to Pool 33. It was necessary to preserve the untagged resident population of this portion of the stream for experiments the following year. Angling was carried out and some returns obtained. Of the eight fish of which no record was obtained three were originally from above Pool 18. It is likely that these fish returned to their home areas and were not recaptured.

ANALYSIS OF DIRECTION OF MOVEMENT

Records of 94 fish of upstream origin were obtained. These actually yield 125 records of movement or failure to move; 66 fish were used once (including 7 which were killed attempting to struggle through the upper screen); 25 were used twice, i.e., these were fish which escaped through the upper screen, were recaptured and replaced in the enclosure to be recorded a second time at the conclusion of the experiment; 3 fish escaped twice and provided three records each. Of the 25 used twice, 3 were killed in a second attempt to traverse the upstream screen.

Out of the 104 downstream trout tagged, 87 were encountered after transfer to the enclosure. Three fish were used twice, giving a total of 90 records. Eleven of these were fish that killed themselves attempting to pass through the screens (2 up and 9 down). The two lots of fish are compared in Table I.

TABLE I. Direction of movement of trout displaced upstream and trout displaced downstream.

	Number of trout		
Origin of trout	No movement	Moved up	Moved down
Upstream	48	71	6
Downstream	40	19	31

Table I shows that 91 per cent of the upstream fish that moved, moved toward home and 62 per cent of the downstream fish moved toward home. That is, in both lots of fish, of those which moved out of the enclosure area, a significantly greater number moved in the direction of their original homes. The greater accuracy of the upstream fish may merely be due to the positive rheotropism of trout in general. However it is also possible to argue that the trout of upstream origin were able to smell their homes while those of downstream origin, unable to smell their homes, made more mistakes in direction.

The next step in the analysis of the records is to examine the relation between period of confinement and subsequent movement.

MOVEMENT IN RELATION TO PERIOD OF CONFINEMENT

It may be seen from the previous section that out of 215 records (90 down plus 125 up) 88 are of trout which remained in the enclosure area after the screens were removed. It is presumed in the argument that follows that these 88 trout had found niches, i.e., established homes, in the enclosure area. In Table II movements in relation to period of confinement are shown.

The data in Table II show that as the period of confinement lengthened, more and more trout remained in the enclosure area. After confinement of 30 days, more than half the trout failed to move when the screens were taken out. From this it is concluded that it takes approximately 30 days for a trout to "forget" home and establish itself in a new area. Contrariwise, it may also be argued that the fish placed in the enclosure during the first 30 days filled the available niches,

and later arrivals were forced to move when given the opportunity. It is not possible to completely dispose of this alternative hypothesis. However, it seems the less likely explanation, for these reasons: all displaced fish attempted to leave the enclosure; fish placed in the enclosure early in the experiment (before available niches were occupied) collected at the screens instead of dispersing throughout the enclosure. Of the 96 fish which left the enclosure after less than 30 days' confinement, only 11 moved in the wrong direction, and these were all fish of downstream origin; of the 31 fish which left the enclosure area after more than 30 days of confinement, 17 moved toward home and 14 moved away from home—almost an equal distribution. The fact that fish confined more than 30 days either failed to move or moved at random suggests strongly that these fish had "forgotten" home. The conclusion seems permissible, then, that fish "remembered" home for 30 days.

TABLE II. Periods of confinement of trout of upstream and downstream origin as related to movement after liberation. Figures in parentheses are percentages.

Time confined days	Number of fish	Remained in enclosure area	Moved toward home	Moved away from home
over 50	31	24 (77)	3	4
40–49	20	13 (65)	4	3
30–39	36	19 (53)	10	7
20–29	56	18 (32)	34	4
10–19	29	5 (17)	23	1
0– 9	43	9 (21)	28	6

SUCCESS IN HOMING

UPSTREAM TROUT. Although the data discussed above reveal a strong tendency for displaced trout to move toward home, they do not indicate how successful they may be in finding home. For this purpose the 71 records of fish which moved upstream (Table I) have been analysed. Seven trout that killed themselves in the upper screen cannot be used; 64 records remain. These must be carefully treated to yield valid information. During August the falling level of Gorge Creek created a filter dam between Pool 2 and Pool 3. Earlier the water had flowed over a collection of waterlogged trash; in August it flowed through it and created a difficult obstacle for the small trout used in this experiment. As a result, 48 records are from Pool 2, only 65 yards above the enclosure. Seven of these fish were originally from Pool 2, i.e., they were home; the remaining 41 came from homes farther upstream. Their presence in Pool 2 after release from the enclosure created an obvious and unnatural crowding and it is beyond question that these fish were held up. This conclusion is strengthened by comparing their weight records with those of the 16 fish which successfully negotiated the obstacle and moved upstream beyond Pool 2. All but one of the 41 fish held up at Pool 2 showed weight losses; the average for the 41 was a loss of 18.5 per cent of their weight. The 16 successful trout showed a net loss of only 2 per cent. (It is normal

for displaced trout to lose some weight (Miller, in press).) It seems logical to conclude that the 41 held-up fish were too weak to surmount the obstacle. They have been eliminated from the analysis of homing success. The 23 usable homing records are shown in Table III arranged according to their distances from home.

TABLE III. Homing success of trout displaced downstream.

Distance displaced	Number of fish	Number reaching home	Distance moved by unsuccessful fish
yards			*yards*
65	7	7	—
165	4	4	—
315	3	2	115
565	1	1	—
825	2	0	565, 565
1,015	1	0	115
1,390	2	0	165, 565
2,090	3	0	565, 565, 725

Table III shows that success in reaching home is a function of distance. Successful or near-successful trout were those whose distances from home were least; the fish which moved the greatest distances were those whose homes were farthest upstream. Time is possibly a factor in the distribution; at most 21 days were available for homing. This may have been too short a time for the fish more than a half-mile from their homes.

DOWNSTREAM TROUT. Thirty-one trout of downstream origin moved or attempted to move downstream from the enclosure area. Eight of these killed themselves in the lower screens and must be omitted from the analysis of homing success. The 23 usable returns are shown in Table IV.

TABLE IV. Homing success of trout displaced upstream.

Distance displaced	Number of fish	Reached home	Fell short	Went too far	Av. distance moved
yards					*yards*
50–150	4	0	1	3	260
250	3	0	0	3	550
400–450	6	1	2	3	435
500–600	6	0	4	2	385
650–750	4	0	4	0	225

Table IV shows that 11 fish went beyond their home pools and 11 failed to go far enough; only one was found in its home pool. Nine that went too far had less distance to go than eight that failed to go far enough. The whole picture is one of complete randomness. Distance travelled bears no relation to distance displaced and the conclusion that these fish were just "drifting" is inescapable. Possibly, after a longer period, the trout would have all drifted below home and then, by smell, have been able to move upstream to home. This is not too

probable, however, as these fish had been at liberty for 19 days; add this period to their times in confinement, and many had been away from home for 30 or more days, long enough to have "forgotten" home.

SIZE OF HOME TERRITORY

The experiment was not designed to throw much light on the question of size of home territory. But some pertinent information was obtained more or less incidentally. Thirty-nine trout, which had been at liberty to move up or downstream, were captured and their tag numbers and localities noted. These were recaptured after varying intervals of time; 8 were recaptured twice and one was recaptured four times. The records are as follows:

23 recaptured in the same place
5 recaptured within 50 yards of the same place
6 recaptured within 100 yards of the same place
1 recaptured 150 yards downstream
1 recaptured 450 yards downstream
3 recaptured 600 yards downstream

These data suggest that cutthroat trout have a fairly limited home range. Twenty-three records show no movement at all; 16 were caught twice, 6 caught three times and 1 caught five times. The time intervals between captures varied from 1 to 55 days; 11 recaptures were after intervals of 1 to 5 days, 11 after 6–10 days, 7 after 11–20 days, and 4 after more than 20 days. The records permit recognition of a change of locality of 10 yards; these 23 trout, then, ranged within an area of 20 yards up and downstream. The other 16 trout show varying degrees of movement which may or may not be normal; repeated capture by angling and confinement in a strange locality may have affected their behaviour pattern.

CONCLUSIONS

(1) Cutthroat trout, transplanted downstream, will attempt to return to their home areas. Very few move in the wrong direction.

(2) Cutthroat trout, transplanted upstream, also attempt to return to their home areas. However, approximately one-third of such trout move in the wrong direction. (Only one-tenth of the trout transplanted downstream made an error of direction.)

(3) Trout transplanted from either upstream or downstream seem to lose their "memory" of home after 30 or more days in a new area.

(4) This 30-day "adjustment" period coincides with the often observed tendency of hatchery-reared trout to drift and be subject to easy capture for 30 or 40 days after planting in a stream.

(5) In this experiment trout of upstream origin displayed some ability to find their homes. This ability appears to be a function of distance; trout closest to home made the best homing records. Trout of downstream origin showed less ability to reach home; the number that failed to go as far as home was the same as the number that went past home.

(6) The observed differences in trout of upstream and downstream origin may possibly be explained by the hypothesis that the sense of smell is the most potent factor in homing. Fish displaced downstream made fewer errors in direction of movement: these fish could smell home continuously. Fish displaced upstream would be unable to smell their homes; many continued upstream on liberation.

The olfactory hypothesis is weakened by the fact that 11 trout drifted below their homes; once reaching home they should have recognized it and remained. However, an hypothesis based on any other sensory perception of home would also be weakened by this finding.

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Stock and Recruitment[1]

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ABSTRACT

Plotting net reproduction (reproductive potential of the *adults* obtained) against the density of stock which produced them, for a number of fish and invertebrate populations, gives a domed curve whose apex lies above the line representing replacement reproduction. At stock densities beyond the apex, reproduction declines either gradually or abruptly. This decline gives a population a tendency to oscillate in numbers; however, the oscillations are damped, not permanent, unless reproduction decreases quite rapidly *and* there is not too much mixing of generations in the breeding population. Removal of part of the adult stock reduces the amplitude of oscillations that may be in progress and, up to a point, *increases* reproduction.

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INTRODUCTION

GENERAL

There exists today a considerable body of knowledge which goes by the name of "the theory of fishing" or "the modern theory of fishing"—the work of a succession of the most distinguished fishery biologists of our time. It is concerned mainly with predicting what catch can be obtained from a given number of young fish recruited to a fishery, if their initial size and the growth and natural mortality rates prevailing are known. That is, methods have been developed for computing the effects of different rates of exploitation, of changes in rate of exploitation from year to year, of different minimum size limits, etc., upon the yield obtained. Not only that, but much progress has been made in developing methods of determining the actual magnitudes of the population statistics required to make these calculations.

Valuable as the above contributions have been, they comprise only half of the biological information needed to assess the effects of fishing and an optimum level of exploitation. Fishing changes the absolute and the relative abundance of mature fish in a stock, and the effect of this upon the number of recruits in future years has often been considered only in the most general manner. The points of view encountered usually range from an assumption of direct proportion between size of adult stock and number of recruits, to the proposition that number of recruits is, for practical purposes, independent of the size of the adult stock. The possibility of a *decrease* in recruitment at higher stock densities has less often been considered.

The scarcity of information on this subject is quite explicable, since it usually requires many years of continuous observation to establish a relation between size of stock and the number of recruits which it produces. However, it has become an urgent problem to have a scientific description of the regulation of abundance of fish stocks, in order to complete the basis for predicting optimum levels of exploitation. This paper attempts to summarize some of the theoretical and factual information available, both from fish populations and from other animals, and to provide a stimulus to studies which will eventually put the subject on a solid foundation.

THEORY OF POPULATION REGULATION

Basic in any stock-recruitment relationship is the fact that a fish population, even when not fished, is limited in size; that is, it is held at some more or less fluctuating level by natural controls. Ideas concerning the nature of such controls were first clarified and systematized by the Australian entomologist Nicholson

(1933). He showed that, while the level of abundance attained by an animal can be affected by any element of the physical or biological environment, the immediate mechanism of control must always involve competition, using that word in a broad sense to include any factor of mortality whose effectiveness increases with stock density[2]. The term *density-dependent* mortality was used for the same concept by Smith (1935). More strictly, density-dependent causes of mortality should include both those which become more effective as density increases and those which become less so. The former are the ones which provide control of population size; and they have been called *concurrent* (Solomon, 1949), *compensatory* (Neave, 1953) or *negative* (Haldane, 1953). The opposed terms are *inverse*, *depensatory* and *positive*, all referring to density-dependent factors which become *less* effective as density increases.

No sharp line can be drawn between the kinds of mortality which are compensatory and those which are not, although Nicholson, Smith and others have felt that as a rule biological factors tend to predominate among the former, and physical agents among the latter, for insects at least. Among fishes, extremes of water temperature, drought and floods, are physical agents which may often cause mortality whose effectiveness is independent of stock density; whereas deaths from such biological causes as disease, parasitism, malnutrition and predation will usually become relatively more frequent as stock density increases. Yet exceptions to the rule above are sufficiently numerous to make the rule itself of doubtful applicability to fishes. For example, the biological factor of predation may have a uniform effectiveness over a considerable range of prey abundance, or at times may even become more effective at lower prey densities; and most if not all physical causes of mortality are compensatory when stock becomes dense enough that some of its members are forced to live in exposed or unsuitable environments. In addition, it is of course often difficult to ascribe a death to any single cause.

There is no necessary relation between the relative magnitudes of the causes of mortality existing at a given time, as measured by the fraction of the stock which each kills, and their relative contribution to compensation. An important and deadly agent of mortality may be strongly density-dependent, or weakly so, or not at all; and different agents may have their maximum compensatory effect over quite different ranges of density.

Age Incidence of Compensatory Mortality

Density-dependent causes of mortality could affect the abundance of either the existing adult stock or the young which it produces. In this paper we will

[2]This almost axiomatic proposition is implied in the writing of various earlier authors back as far as Malthus, but Nicholson was the first to formulate it explicitly and to emphasize its importance: Haldane (1953) calls his inspiration "a blinding glimpse of the obvious". The theorem and its diverse consequences were elaborated mathematically by Nicholson and Bailey (1935). Subsequent writers have developed it with varying emphasis, but nothing very substantial seems to have been added. Solomon (1949) gives a useful review of this literature, and Varley's (1947) quantitative assessment of various agents controlling the abundance of a trypetid fly population is outstanding.

consider mainly the effects of density dependence in the mortality which strikes the younger members of a population—among fishes, the eggs, larvae, fry and fingerlings. That is, the relative abundance of a brood will be considered to be determined by the time the first of its female members begin to mature: subsequent mortality is assumed to be non-compensatory.

This distinction between immature and mature stages of the life history, and the restriction of compensatory mortality to the former, is the principal difference between the thesis of this paper and that of earlier treatments of effects of density upon reproduction (e.g., Hutchinson, 1948; Haldane, 1953; Fujita and Utida, 1953; and many others). These have usually taken the Verhulst logistic equation as a point of departure:

$$\frac{dN_t}{dt} = \frac{bN_t(K - N_t)}{K}$$

(N_t is abundance at time t; K is equilibrium abundance; b is the instantaneous rate of increase of the population at densities approaching zero.) This expression implies a continuous tendency for the population to adjust itself toward the equilibrium size K, whether it is currently less than or greater than K. The adjustment would evidently have to involve compensatory mortality among the adult stock when its density is greater than K. Though such mortality is not impossible, there is in fish populations, at least, little indication of it; and as a matter of fact this aspect of the logistic equation has never been applied to any concrete biological situation.

Our assumption that *no* compensatory mortality occurs among the mature stock is unlikely to be strictly true of any species, and may not be even approximately true of some. Nevertheless it has seemed worth while to follow out the consequences of making this distinction between mature and immature, with fishes particularly in mind. The opportunities for compensatory effects are so much greater during the small, vulnerable early stages of a fish's life, that restriction of compensation to those stages seems likely to have wide applicability as a useful approximation.

To further simplify the initial approach to the problem, fishing is considered to attack only mature individuals, so that the ***recruitment*** produced by a given density of mature stock means both the number of commercial-sized fish, and the number of maturing fish, which result from its reproductive activity. The term *reproduction* will be used in a similar but slightly more general sense, to mean the number of young surviving to any specified age after compensation is practically complete; it will *not* mean the initial number of eggs or newborn young.

The above conditions and definitions will be assumed to apply unless exception is made specifically.

Kinds of Population Control Mechanisms

Compensatory types of mortality can be of various kinds. Some of the more likely possibilities are as follows:

1. Prevention of breeding by some members of large populations because

all breeding sites are occupied. Note that territorial behaviour may restrict the number of sites to a number less than what is physically possible.

2. Limitation of *good* breeding areas, so that with denser populations more eggs and young are exposed to extremes of environmental conditions, or to predators.

3. Competition for living space among larvae or fry, so that some individuals must live in exposed situations. This too is often aggravated by territoriality—that is, the preemption of a certain amount of space by an individual, sometimes more than is needed to supply necessary food.

4. Death from starvation or indirectly from debility due to insufficient food, among the younger stages of large broods, because of severe competition for food.

5. Greater losses from predation among large broods because of slower growth caused by greater competition for food. It can be taken as a general rule that the smaller an animal is, the more vulnerable it is to predators, and hence any slowing up of growth makes for greater predation losses. Since abundant year-classes of fishes have often been found to consist of smaller-than-average individuals (Hile, 1936), this may well be a very common compensatory mechanism among fishes (cf. Ricker and Foerster, 1948; Johnson and Hasler, 1954).

6. Cannibalism: destruction of eggs or young by older individuals of the same species. This can operate in the same manner as predation by other species, but it has the additional feature that when eggs or fry are abundant the adults which produced them tend to be abundant also, so that percentage destruction of the (initially) denser broods of young automatically goes up—provided the predation situation approaches the type in which kills are made at a constant fraction of random encounters (cf. page 609, below).

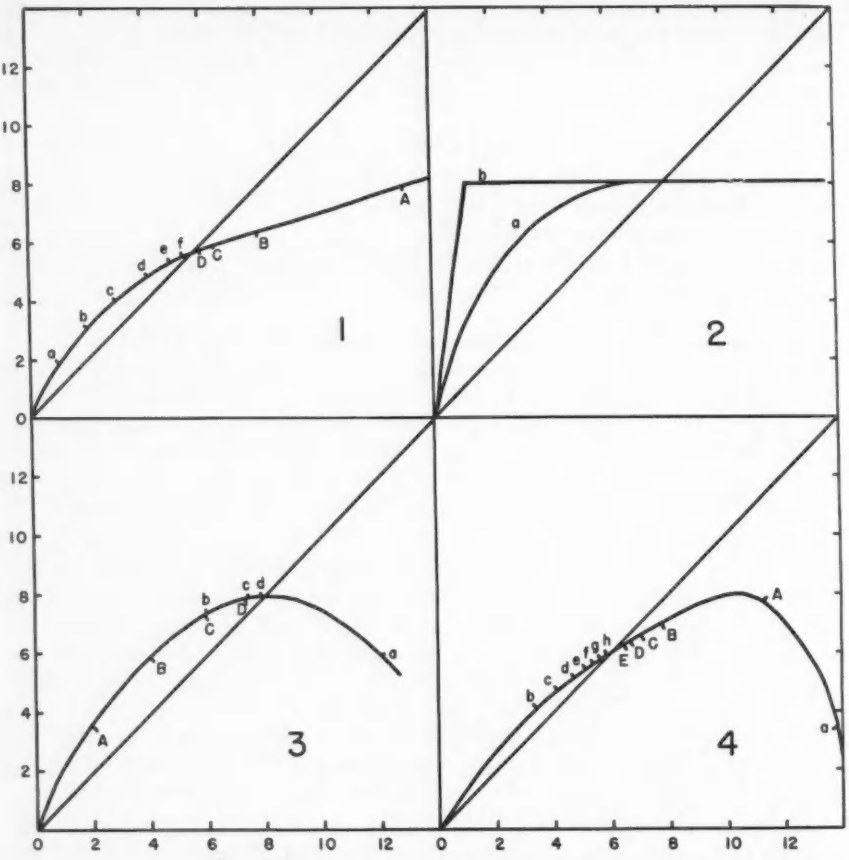
7. Larger broods may be more affected by macroscopic parasites or microorganisms, because of more frequent opportunity for the parasites to find hosts and complete their life cycle.

8. In limited aquatic environments there may be a "conditioning" of the medium by accumulation of waste materials that have a depressing effect upon reproduction, increasingly as population size increases.

Not all of the above compensatory effects need exist, or be important, in any given population, or in the same population every year. To a considerable extent they are likely to be complementary, so that if, for example, exceptionally favourable conditions permitted a good hatch of even a large spawning of eggs, a reduced growth rate of the fry would permit increased predation and so reduce survival in that way.

TYPES OF REPRODUCTION CURVES

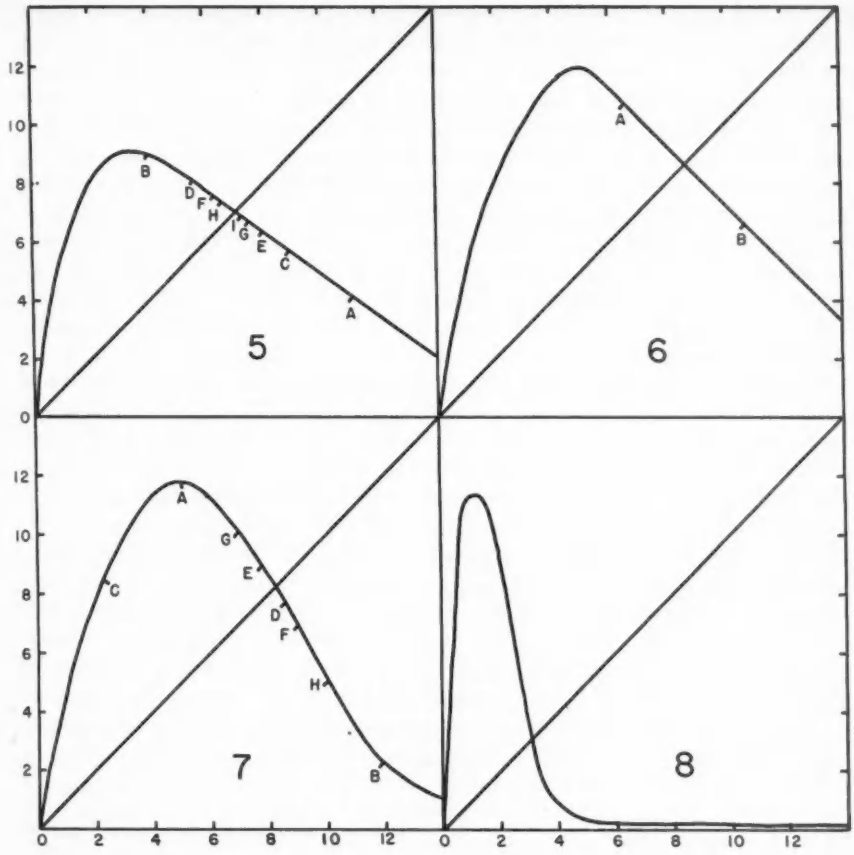
Whatever the various kinds of compensatory and non-compensatory mortality acting on a brood may be, the average resultant of their action, over the existing range of environmental conditions, is represented by the average size of maturing brood, or recruitment, which each stock density produces. A graph of this relationship between an existing stock, and the future stock which the existing



FIGURES 1–4. Stock-reproduction relationships characterized by a stable equilibrium. *Abscissa*– number of eggs produced by parent stock in a given year; *ordinate*–number of eggs produced by the progeny of that year.

stock produces, will be called a "reproduction curve". It is most convenient to label the axes in terms of the *eggs* in present and future generations, respectively[3]. The abscissa represents the mature eggs produced by the current year's stock. The ordinate represents the total of mature eggs produced by the progeny re-

[3]The argument is developed here in terms of populations of oviparous fishes which spawn once a year, but it can readily be modified to apply to other kinds of animals; an example for a viviparous animal is given on page 596. Among mammals, choice of the most suitable census age for plotting on reproduction curves may require care. If newborn young are used, effects of stock density upon frequency of conception and uterine mortality may be overlooked. If number of mature females is used, it should preferably be adjusted to take care of age variation in litter size or frequency, as the age structure of the population changes.



FIGURES 5–8. Stock-reproduction relationships in which there is an oscillating equilibrium, or (in 5) an oscillating approach to stable equilibrium. Axes as in Figures 1–4.

sulting from the current year's reproduction (obtained by summing over such period of time as the current year's hatch is a component of future years' stocks). In a state of nature, or with a stable fishery, the average size of parental and filial egg production, defined as above, tends to be equal over any long period of years, although striking changes may occur between individual years, or generations.

Figures 1–8 show a number of possible types of reproduction curve. In each of them the straight diagonal constitutes a useful boundary of reference which will be called the "45-degree line". Any curve lying wholly above this line describes a stock which is increasing without limit, hence such a curve cannot exist in practice. Similarly a curve below the 45-degree line describes a stock

that will decrease to zero in a few generations[4]. The 45-degree line itself would describe a stock in which density dependence is absent, the filial generation tending always to be equal to the parental, except as factors independent of density deflect it. Such a stock would have no mechanism for the regulation of its numbers: if only density-independent causes of mortality exist, the stock can vary without limit, and must eventually by chance decrease to zero. Thus the first qualification of a reproduction curve is that it must cut the 45-degree line at least once—usually only once—and must end below and to the right of it.

Figures 1–8 indicate some of the types of recruitment curve that might exist in actual populations. All are characterized by having a region above the 45-degree line in which reproduction is more than adequate to replace the existing stock, and a region below the 45-degree line in which reproduction is inadequate to replace existing stock.

In the population of Figure 1, rate of reproduction (ratio of filial to parental eggs) decreases continuously as size of stock increases, although the slope of the curve becomes stabilized soon after the 45-degree line is crossed, and the actual number of young produced continues to rise indefinitely. Beyond the 45-degree line, however, this number is inadequate to fully replenish the stock.

In the population of Figure 2a, rate of reproduction also declines continuously; the actual number of recruits produced reaches an asymptotic level and thereafter does not change. Curve 2b differs from 2a in that it rises more steeply and it is initially straight; i.e., at low stock densities rate of reproduction is large, and constant. The range of densities over which there is constant recruitment is quite broad in b, simulating the condition loosely described by the statement "there are always as many recruits as the grounds can support".

Figures 3–8 show reproduction curves in which numbers of recruits begin to decrease after stock reaches some large magnitude. Such curves have an ascending left limb, a dome and a descending right limb. The descending right limb provides of course a more severe control of stock size at the higher densities. The differences in position of the dome and in the slope of the two limbs are of importance in determining changes in stock abundance, as described below.

All these curves are meant to represent the net effect of the sum total of density-dependent mortality factors acting upon the population. The reproduction of any actual year is affected also by density-independent factors, so that the actual number of young produced will deviate from the number indicated by the curve. In a later section the effect of such density-independent factors will be

[4]This statement is likely to be literally true only if the reproduction curve is plotted and fitted on logarithmic axes. On arithmetic axes a curve lying wholly below the 45-degree line *could* describe a stable population (having more than one age in the breeding stock) provided there were moderate to large random deviation from the average relationship. This point is discussed further on page 578, where it is evident that it would be advantageous to fit reproduction curves on logarithmic axes so that deviations above and below the curve would be in better balance. However such plotting has the serious disadvantage that statements of parent-progeny relationships in terms of the slopes of the two limbs of the curve become too complex to be practical. The best way out of this difficulty would be to fit the curve on a logarithmic plot, then transform it to arithmetic axes for interpretation.

examined. The first task will be to consider how a population behaves, under the strict control of a reproduction curve, when it is given some initial randomly chosen position.

This subject, and others later, will be considered for two situations separately. The first is where the currently hatched brood will constitute the whole of the breeding stock of a subsequent generation; that is, there is no mixing of ages in the spawning stock. This situation is fairly common among insects; for example, many mayflies, stoneflies, caddis flies, etc., have a single brood per year, usually with a one-year life cycle. Among vertebrates this condition is exceptional, but it exists in some fishes. There the length of life is commonly more than one year, so that two or more separate populations or "lines" exist concurrently.

The other situation to be considered is of course that where two or more broods contribute to the spawning stock at any given moment. Among vertebrates at least, this is the usual state of affairs.

REPRODUCTION IN THE ABSENCE OF DENSITY-INDEPENDENT VARIABILITY

Single-Age Spawning Stocks

In all of the relationships shown in Figures 1–8, the stock is in equilibrium at the density at which the reproduction curve cuts the 45-degree line—that is, the stock is then producing enough progeny, and only enough, to replace its current numbers. In Figure 1, an initial deflection of abundance to either side of the equilibrium point is compensated by a gradual, asymptotic return to equilibrium, for example by paths A–D or a–f. In Figure 2a things work the same way to the left of the equilibrium point; to the right of it any deflection, no matter how great, is returned to equilibrium in a single generation. In Figure 2b deviations to the left, as far as 1.5 units of stock, are also returned immediately to the equilibrium level.

In Figure 3 the equilibrium point is at the top of the dome of the reproduction curve. The curve resembles 1 as regards deflections to the left of the equilibrium point; but a displacement to the right is followed by an immediate return across the 45-degree line to the ascending limb, after which it "climbs" this limb to the equilibrium point (a–d). The curve of Figure 4 is similar, but the dome lies to the right of the 45-degree line; A–E and a–h are possible paths to the equilibrium point.

In Figure 5, a stock deflected from equilibrium to any position along the descending limb will oscillate back and forth about the equilibrium point with decreasing amplitude, for example by the route A–I. If the deflection is great enough, the stock may have to climb the left limb before it is swung over to the right limb and begins the oscillating phase.

In Figure 5 the right limb has a downward (negative) slope numerically less than −1. In Figure 6 this slope is exactly −1 after the dome is passed. Here any moderate deflection along the straight part of the right limb results in a swing back across the 45-degree line of exactly the same magnitude, so that the deflection tends to be perpetuated indefinitely; for example, A and B are two such

conjugate points. The intersection of the 45-degree line is a point of "indifferent" equilibrium; it is itself stable, but there is no inherent tendency for the stock to return to that level.

Finally, when the slope of the right limb of a reproduction curve lies between -1 and $-\infty$, equilibrium at the 45-degree line is not merely indifferent, it is unstable. That is, any deflection from equilibrium, no matter how small, initiates a series of oscillations along the right limb whose amplitude increases until the dome of the curve is reached or surpassed. The latter event usually sends the stock back to the right limb and the cycle begins again. No matter where they begin, all such cycles eventually reach the dome of the curve, and a stable oscillation series is established for which the dome is a convenient starting point. The cycle in Figure 7 is A, B, C, D, E, F, G, H, A, etc. (cf. Fig. 11D, below); the number of stages in this cycle depends upon the exact shape of the curve, chiefly upon whether or not one stage lands close to the 45-degree line. Figure 8 represents a more extreme situation, in which substantial reproduction is obtained over only a narrow range of stock densities considerably below the equilibrium level, and the stock would be subject to violent oscillations.

Multiple-Age Spawning Stocks

When a spawning population consists of two or more age-groups, the young produced in a given year contribute to the stock of more than one future year, and the results of a deflection from equilibrium abundance are much modified. A fairly plausible example is where each brood contributes to the spawning stocks of four future years, in the ratio 2:3:3:2, and first spawning occurs 4 years after a brood was produced (Table I). Figure 9 shows the result of an initial deflection of such a stock to an abundance of 12, on some of the reproduction curves of Figures 1–8. The course of events for the most part reflects what was learned in the single-spawning situation. Those based on Figures 1–6 all end up at the stable equilibrium level; this being reached by direct approach for 1, 2 and 3, with one hesitation for 4, and by a series of damped oscillations for 5 and 6. From Figures 7 and 8 series of undamped oscillations are obtained, that is, permanent cycles of abundance.

It may seem surprising that curve 6 too does not generate permanent oscillations, but the mixing of year-classes gradually brings the stock to a steady level, in the absence of any tendency toward divergence.

The permanent oscillations of the type produced by curves 7 and 8 will repay more extended discussion. Figure 10 depicts series of oscillations, based on Figure 7, but with each brood contributing to the spawning stock for only two years. Time of first maturity is successively delayed one, two and more years, so that the average contribution to reproduction is made 1.5, 2.5, 3.5, etc., years after the brood in question existed as mature eggs. In every case stable cyclical fluctuations exist, just as in Figure 9F. Their *period* is always double the mean interval from egg to egg, that is, 3, 5, 7, etc., years.

The *amplitude* of the cycle varies. If the fish spawn first in the year after their appearance, amplitude is very small, but it quickly increases if maturity

TABLE I. An illustration of how to obtain the definitive distribution of population abundance for given conditions and a given reproduction curve, in this case Figure 7. Four years are assumed to elapse between a brood's existence as fertilized eggs and its first year of contribution to reproduction, while its total egg production is divided among the 4 successive years of its mature existence in the ratio 2 : 3 : 3 : 2. An arbitrary stock density (measured in terms of its egg production) is taken as a starting point, in this case 2.0 units (column 5). The reproduction corresponding to this abscissal value is read off from the ordinate of Figure 7, namely 7.9 egg units (column 6). These eggs are divided among the 4 years in which they are actually laid, beginning 4 years after the year in which the fish that carry them were hatched. For example, the 10.2 units of "recruitment" in line 5 are divided among line 9 (2.0 units), line 10 (3.1 units), line 11 (3.1 units), and line 12 (2.0 units). Breeding potential for each year (column 5) is obtained by horizontal addition of the contributions of the 4 age-groups in columns 1–4. In this example the definitive 11-year period of oscillation is achieved in the first peak-to-peak interval, while the average definitive amplitude, approximately 3.6 to 11.3, is apparent in the second peak-to-peak interval. Adjustment to the conditions imposed by the reproduction curve is not always as rapid as this.

Eggs produced at successive ages						Eggs produced at successive ages					
IV	V	VI	VII	Stock	Recruitment	IV	V	VI	VII	Stock	Recruitment
0.4	0.6	0.6	0.4	2.0	7.9	0.6	1.3	2.0	2.0	5.9	11.4
0.4	0.6	0.6	0.4	2.0	7.9	0.6	0.8	1.3	1.4	4.1	11.5
0.4	0.6	0.6	0.4	2.0	7.9	1.0	0.9	0.8	0.8	3.5	10.7
0.4	0.6	0.6	0.4	2.0	7.9	1.7	1.4	0.9	0.6	4.6	11.8
1.6	0.6	0.6	0.4	3.2	10.2	2.3	2.6	1.4	0.6	6.9	10.3
1.6	2.4	0.6	0.4	5.0	11.9	2.3	3.4	2.6	1.0	9.3	6.4
1.6	2.4	2.4	0.4	6.8	10.4	2.1	3.4	3.4	1.7	10.6	4.2
1.6	2.4	2.4	1.6	8.0	8.7	2.4	3.2	3.4	2.3	11.3	3.1
2.0	2.4	2.4	1.6	8.4	8.0	2.1	3.5	3.2	2.3	11.1	3.5
2.4	3.1	2.4	1.6	9.5	6.1	1.3	3.1	3.5	2.1	10.0	5.3
2.1	3.6	3.1	1.6	10.4	4.6	0.8	1.9	3.1	2.4	8.2	8.3
1.7	3.1	3.6	2.0	10.4	4.6	0.6	1.3	1.9	2.1	5.9	11.4
1.6	2.6	3.1	2.4	9.7	5.8	0.7	0.9	1.3	1.3	4.2	11.6
1.2	2.4	2.6	2.1	8.3	8.2	1.1	1.0	0.9	0.8	3.8	11.1
0.9	1.8	2.4	1.7	6.8	10.4	1.7	1.6	1.0	0.6	4.9	11.9
0.9	1.4	1.8	1.6	5.7	11.5	2.1	2.5	1.6	0.7	6.9	10.3
1.2	1.4	1.2	1.2	5.2	11.9	2.3	3.1	2.5	1.1	9.0	7.0
1.6	1.7	1.4	0.9	5.6	11.7	2.2	3.5	3.1	1.7	10.5	4.4
2.1	2.5	1.7	0.9	7.2	9.9	2.4	3.3	3.5	2.1	11.3	3.1
2.3	3.1	2.5	1.2	9.1	6.8	2.1	3.6	3.3	2.3	11.3	3.1
2.4	3.5	3.1	1.6	10.6	4.2	1.4	3.1	3.6	2.2	10.3	4.8
2.3	3.6	3.5	2.1	11.5	2.8	0.9	2.1	3.1	2.4	8.5	7.8
2.0	3.5	3.6	2.3	11.4	3.0	0.6	1.3	2.1	2.1	6.1	11.2
1.4	3.0	3.5	2.4	10.3	4.8	0.6	0.9	1.3	1.4	4.2	11.6
0.8	2.0	3.0	2.3	8.1	8.5	1.0	0.9	0.9	0.9	3.7	11.0

is delayed. More generally, appreciable amplitude in cycles of this type depends upon a preponderance of the reproduction of a brood occurring after one or more spawning periods have elapsed from the time of its birth.

With the longer intervals of lag between hatching and first spawning the cycles of Figure 10 become less regular; minor peaks appear, and the pattern is duplicated more closely at 2-cycle intervals, a feature which can be detected also in Figure 9F. However, these tendencies are much less apparent when more than two ages occur in the spawning stock, and only the dominant peaks would be detectable with any combination of average age of spawners and average age at first maturity that is apt to occur in nature.

Endless examples of reproduction-curve cycles can be constructed. Any desired combination of period and amplitude can be obtained, in more than one way, by selecting appropriate combinations of reproduction curve and age distribution of breeding. The general characteristics of such cycles can be summarized as follows:

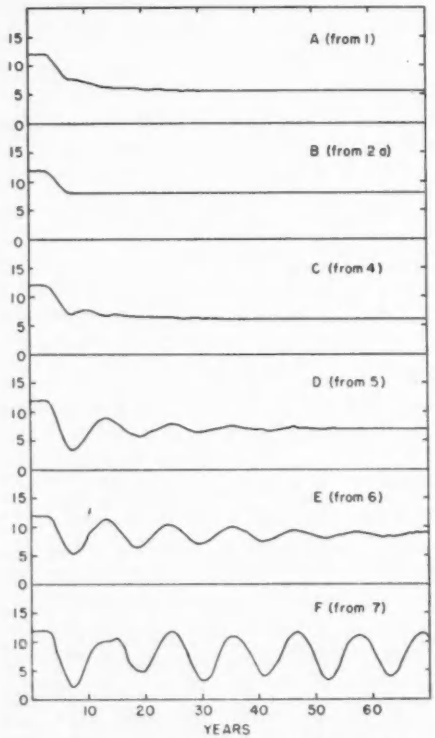


FIGURE 9. Change in abundance of the stocks of Figures 1, 2a and 4–7, following an initial sustained deflection to an abundance of 12 units, when the spawning stock is composed of 4 year-classes and first spawning is in the fourth year after hatching. *Abscissa*–years (generations); *ordinate*–relative abundance (egg production) of the mature stock.

1. Cycles occur when the outer part of the reproduction curve slopes downward, provided this slope begins at some point above the 45-degree line.

2. Cycles are damped and eventually disappear when the slope of the outer limb of the reproduction curve lies between 0 and —1. They are permanent when the slope is numerically somewhat more than —1, the exact critical limit depending upon the amount of mixing of generations in the spawning stock and the interval to first spawning.

3. Period of oscillation is determined by the mean length of time from parental egg to filial eggs, being twice that interval or close to it. It is independent of the exact shape of the reproduction curve, and also independent of the number of generations in the spawning stock, provided there is more than one.

4. Amplitude of oscillation depends partly on the exact shape of the reproduction curve.

5. Amplitude of oscillation tends to decrease with increase in the number of generations comprising the spawning stock.

6. Amplitude of oscillation increases rapidly with increase in number of generations between parental egg and the first production of filial eggs, up to a

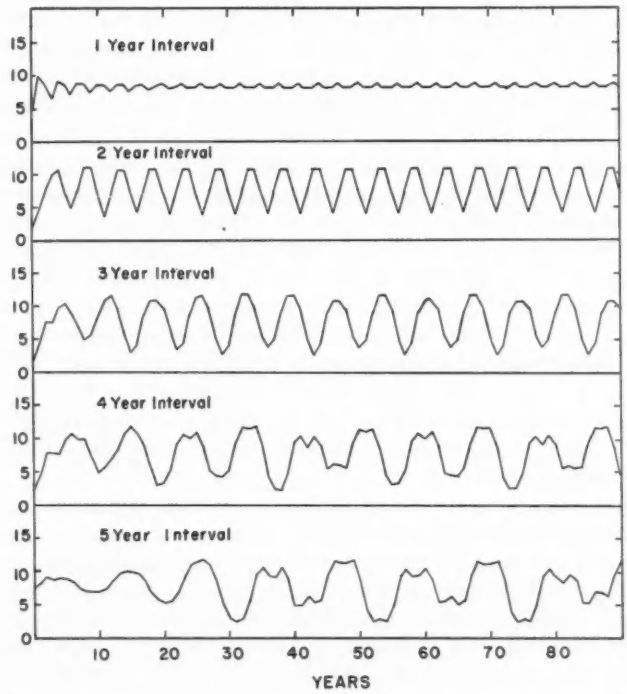


FIGURE 10. Population oscillations determined by the reproduction curve of Figure 7, when there are two ages in the spawning stock and spawning first occurs after 1, 2, 3, 4 and 5 years, respectively, from deposition of the parental eggs. Axes as in Figure 9.

limit imposed by the shape of the reproduction curve. When reproduction by a brood begins strongly in the generation following its birth, the oscillations are so weak that they could not be recognized in practice.

VARIATIONS IN REPRODUCTION PRODUCED BY FACTORS INDEPENDENT OF DENSITY

General

A comparison of density-dependent and density independent reproduction is desirable in order to find possible means of distinguishing the two by their effects on population abundance, particularly since it has been suggested that some of the apparently periodic variations in animal numbers may reflect random variability alone (Hutchinson, 1948; Palmgren, 1949; Cole, 1951, 1954).

As an introduction, it is known that quantitative events selected completely at random tend to have an average peak-to-peak interval of exactly 3, provided they are classified finely enough that like values do not occur in adjacent positions. Cole (1951) demonstrates this mathematically and found approximately this period in a selection from Tippett's table of random numbers.

Cole uses a sequence of Tippett's numbers as a model with which to compare cycles of animal abundance in nature. Such a model, however, is not appropriate for our present purpose, because it must be interpreted as a reflection of random variation in the capacity of the environment to sustain the animal in question, rather than random variation in number of mature progeny produced per female. This is true for the following reason. When using Tippett's table or any similar assemblage, the number of numbers available is finite. The smallest number can as easily be followed by the largest as by any other; the largest cannot be followed by anything larger. The biological characteristics of a corresponding population are that it must have a very large potential rate of increase (since the greatest possible abundance can follow directly on the least), and it must have severe compensation at the higher stock densities (since they are close to a ceiling of abundance which cannot be exceeded). Few if any populations could meet both these conditions in the course of a single reproductive period, so that Cole's model, to have verisimilitude, must be applied only to situations where a census is taken at intervals of several generations. Thus it is not appropriate, for example, to fish populations when censused yearly, since these usually spawn only once a year.

In any event, a simple series of random numbers is not a suitable model of random variation *in success of reproduction*. What then *is* a suitable model? Since extremes of environmental conditions are less common than conditions approaching normal, our first postulate will be that a normal frequency distribution provides a fairly realistic picture of the relative frequencies of the resultants of the various independent factors making for success or failure in reproduction; from which resultants a random selection is to be made. Table 8.6 of Snedecor (1946) was used for this purpose, selection of t-values being made corresponding to the figure in the ".00" column closest to each of a sequence of selections from Tippett's random table. The series obtained begins as follows: 1.8, 0.5, 0.2, 0.1, 0.2, 0.0,

1.0, 0.1, etc. Tippett's table was again used to divide these into items representing reproduction above and below the replacement level, respectively; this gave the series below, decreases being followed by *d*.

1.8*d*, 0.5, 0.2, 0.1, 0.2*d*, 0.0, 1.0*d*, 0.1, etc.

The next question is to decide how these are to be applied to an existing reproductive potential. An illustration will be of assistance. Suppose that a breeding population matures 10 billion (10^9) eggs; and let us define "average" environmental conditions here as those which will permit the maintenance level of reproduction, that is, 10 billion future mature eggs produced by the progeny of the current year's sexual activity. Variations in environmental conditions add to or delete from this average production. The most severe conditions imaginable can reduce reproduction to zero. The most favourable conditions possible will permit the survival of all the eggs and thus, assuming equality of the sexes, produce future reproductive units to the number of 5 billion times the total expectation of egg production of a female fish just maturing—which expectation might easily be 2,000,000 in the case of the cod, for example. The mean and the extreme limits of reproduction would thus be:

	Mature eggs	*No. of fish (at first maturity)*
Lower limit:	0	0
Average:	10,000,000,000	10,000
Upper limit:	10,000,000,000,000,000	10,000,000,000

This shows that in a fairly typical instance the stock produced by average environmental conditions is located very asymmetrically with respect to the two extreme limits, on this arithmetic scale. On a logarithmic scale the average production becomes much more nearly central, if a minimum of 1 fish is assumed:

	Log No. of fish
Lower limit:	0
Average:	4
Upper limit:	10

From this and other considerations it appears likely that our symmetrically distributed environmental variations will tend to act in relative rather than absolute fashion; so that, for example, if a given negative deviation produces a decrease in reproduction to half of the average level, the same positive deviation will increase reproduction to twice the average level. In other words, the figures representing environmentally caused deviations from the reproductive norm must be multiplicative rather than additive. To put them into this form, unity is added to each, so that deviations indicating below-average conditions (the *d*-items above) become divisors, those indicating above-average conditions become multipliers, and zero deviation is multiplication or division by unity. The result is shown in Table II. The absolute magnitude of the items shown is of course arbitrary, and it can be varied at will by multiplying the original random series (before unity was added) by any desired integer or fraction.

TABLE II. Series of numbers selected randomly from a population having the positive half of a normal frequency distribution with a standard deviation of unity, each number augmented by unity, and the series divided randomly into multipliers and divisors (the latter indicated by the suffix "*d*").

2.8*d*	1.1*d*	3.0*d*	2.2	1.9*d*	1.3*d*
1.5	1.1*d*	1.9	1.1*d*	1.0	1.6*d*
1.2	1.9*d*	1.4	1.0	2.0*d*	1.2
1.1	2.0*d*	1.1	1.4	1.1*d*	2.2*d*
1.2*d*	2.4	2.4*d*	1.7*d*	2.8	1.3*d*
1.0	1.5*d*	1.7*d*	1.7*d*	2.7	2.3*d*
2.0*d*	2.2	1.3	1.6	2.8*d*	1.2
1.1	1.3*d*	2.7*d*	1.8	3.5*d*	1.3
2.3*d*	1.2	1.5*d*	1.4*d*	1.2*d*	3.0
1.8*d*	1.9	1.9	1.0	1.2*d*	1.3
1.1*d*	2.0*d*	1.9*d*	1.8	1.7	2.2*d*
1.7	2.1*d*	2.1*d*	1.0	1.9*d*	3.2*d*
1.8*d*	1.5	1.8*d*	2.2	2.6	1.4*d*
2.5	1.3*d*	1.8	1.0	2.4*d*	1.5
2.0	1.6*d*	2.6*d*	1.5*d*	2.5	1.9*d*
2.0*d*	1.5*d*	2.3	2.2*d*	2.0*d*	1.1*d*
2.0	1.0*d*	1.7*d*	1.6*d*	2.2*d*	2.6
2.2*d*	1.9*d*	1.1	1.9	2.1*d*	2.5
2.2	1.9*d*	2.8	1.7	1.9	2.1*d*
1.3	1.3	1.3	2.6	1.8*d*	2.6*d*
1.4	2.1*d*	1.1*d*	2.4*d*	2.8	2.1*d*
1.2*d*	2.1	1.6	1.5	1.3	1.8
2.0*d*	1.2	1.2*d*	2.0*d*	1.7*d*	2.6*d*
1.7*d*	1.8	1.0*d*	1.7*d*	1.6	1.3
1.1*d*	2.0	1.7	1.0	1.7*d*	2.5*d*
1.5	1.1*d*	1.4	1.2*d*	1.8	2.7*d*
2.2	2.3	1.1	1.5	1.0	1.1
1.6	1.2	2.1*d*	2.0	2.0*d*	1.3
1.4*d*	2.0*d*	2.1	1.3*d*	2.0	1.7*d*
2.0*d*	1.6*d*	1.9*d*	1.8*d*	1.6	1.1*d*
1.3*d*	2.4*d*	1.2*d*	2.3	1.0*d*	2.0
3.4	1.1*d*	1.1*d*	1.6	1.3*d*	1.6
1.3	1.7*d*	1.6	1.3*d*	3.7*d*	3.3*d*
3.2*d*	1.9*d*	1.5*d*	1.7*d*	1.3	2.3*d*
1.3	2.7*d*	1.3	1.3*d*	1.0	1.5*d*
2.2*d*	1.5	2.2*d*	1.7	1.3	1.6*d*

SINGLE-AGE SPAWNERS

Since the figures of Table II constitute a model of variation in success of reproduction under the influence of density-independent factors alone, a picture of corresponding population fluctuations is obtained by multiplying some initial stock density by each item in succession. This is done in the lower line of

Figure 11A; the upper line is from a different random series. The lines fluctuate a good deal and at times diverge considerably from the original abundance: at the end of the 70 generations shown in Figure 11 the Table II line has changed by a factor of 260; while if the same is continued through the whole 216 generations of the Table the net change is 5.5×10^{-7}, representing a relative decrease

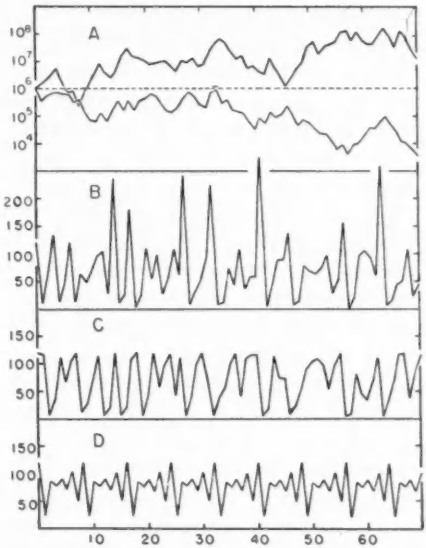


FIGURE 11. Fluctuations in ideal populations of single-age spawners. *Abscissa*—generations; *ordinate*—number of units of stock.

A. Two series of changes in a population from an initial density of 1,000,000, when it varies under the influence of density-independent factors only. The lower line corresponds to the first 70 entries of Table II, multiplied in sequence.

B. Changes in a population from an initial abundance of 119, as determined by the random factors of Table II and the reproduction curve of Figure 7, when the action of the latter precedes the former.

C. As in B, but with the random factors acting before the compensatory mortality shown by the reproduction curve.

D. Population cycle generated by Figure 7 alone.

from 55,000,000 to 1. This large change occurs in spite of the fact that Table II is constructed in such a way that, if it were continued over any really long period, the population should be above its initial level about as often and as much as it is below it[5]. The net change results partly from an excess of d-items in Table II, and partly from the fact that the d's happen to be larger numbers, on the whole.

[5]A series of 1,000 "generations" constructed in a different but analogous fashion by Hutchinson and Deevey (1949, fig. 4) shows similar major long-period trends.

By chance the change indicated by Table II is considerably greater than would be expected to occur often in a series of only 216 generations. However it is easy to show that as the number of generations increases, the most probable divergence of population size from the original level also increases continuously. When the number of generations approaches anything appropriate to a geological time scale the likely change is very great indeed. For example, after 10,000 generations the standard deviation of the number of increases (or decreases), from the most probable number 5,000, is $\sqrt{10{,}000} \times \frac{1}{2} \times \frac{1}{2} = 50$. This means that there is about 1 chance in 3 that the excess of increases or decreases will be 50 or more at that time, while the chances of the excess having been 50 or more at some time *during* the 10,000 generations are much greater. With an average change factor of 1.67 from one generation to the next (as in Table II), this means that the population is fairly certain to have been increased or decreased by a factor of about 1.67^{50}, or 140,000,000,000, somewhere along the line. Without wasting thought on the impossibility of a population of any sizable organism *increasing* this much, such a *decrease* would obviously bring even the most numerous fish stock, for example, to extinction. Thus no population of single-age spawners can survive if its reproduction is completely at the mercy of density-independent influences in the environment. In the same way a gambler will in the long run lose everything if his opponent has equal skill and unlimited resources. (In practice, of course, the effects of random environmental factors would usually vary as between different parts of the animal's range, and local extinction could be followed by recolonization from adjacent areas.)

The average interval between peaks of Table II should be close to the 3 which is characteristic of a random series; in actuality it was 3.09 when ties were randomly divided into higher and lower values. However this is not what determines the period of a series such as Figure 11A. In the latter a peak occurs whenever a multiplier is followed by a divisor, and the average interval between peaks is nearly 4 years, again adjusting for ties. The theoretical or long-term average period can be determined as follows: since a peak or trough occurs whenever there is a change from multiplier to divisor or divisor to multiplier, the expectation that the first such change will occur between adjacent cells is one-half, the expectation that it will occur between a cell and the next but one is one-fourth, that it will occur at the third cell is one-eighth, and so on. The average of these intervals 1, 2, 3, etc., weighted as to frequency, is exactly 2, which represents the average peak-to-trough interval. Since peaks and troughs are equally common, the average peak-to-peak or trough-to-trough interval is therefore 4.

However it must be emphasized that this 4 represents the average interval between *all* peaks, regardless of size. Casual inspection of Figure 11A might give a different impression. The eye tends to ignore the smaller humps, and to impose a certain regularity among the rest by magnifying those of intermediate size when they happen to fall into a sequence with large ones, and diminishing them when they do not. In this manner the lower line could "suggest" a cycle of 11 or 12 years, with 4 peaks and 4 troughs actually showing.

Multiple-Age Spawners

To obtain a model of the consequences of random fluctuations upon reproduction of multiple-age stocks, the random values of Table II have been applied to a "population" constructed on the same basis as Figure 9—that in the spawning stock there are 4 ages, that each year-class produces eggs in the ratio 2:3:3:2 in the 4 years of its reproductive activity, and that each fish spawns for the first time 4 years after it was itself a fertilized egg. The resulting curve is shown in Figure 12A (it starts from an age distribution characteristic of the reproduction-curve cycle of 12D).

The most distinctive characteristic of the line of Figure 12A is that it tends to rise. This increase occurs in spite of the fact that divisors happen to be in excess in Table II, and if the series is continued a little farther much higher values are encountered. The fact is that, if continued, the population will increase without limit. The reason is that the contributions of the several year-classes to a given year's spawning must be added arithmetically, while expectation of

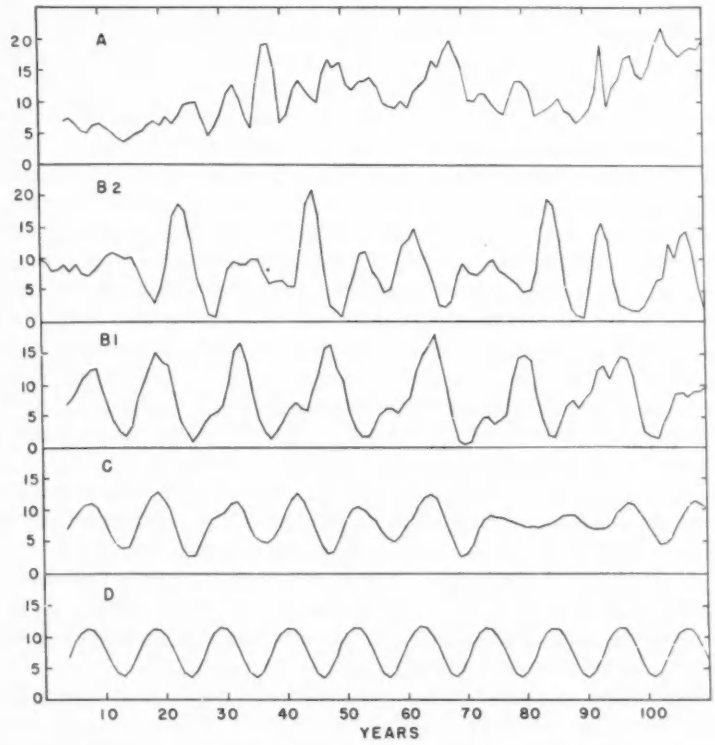


Figure 12. Fluctuations in a population of multiple-age spawners, as determined by the random series of Table I (curve A), by the reproduction curve of Figure 7 (curve D), and by combinations of these (curves B and C). Axes as in Figure 9.

survival of an egg is proportional to random environmental effects having a symmetrical distribution so constituted that any increase is greater, absolutely though not relatively, than the corresponding decrease. It would be difficult, of course, to prove that environmental effects upon reproduction are actually distributed in just this manner. On the other hand it was shown above that they are very unlikely to be merely additive; and any intermediate condition will result in a slower but still unlimited upward trend to a graph such as Figure 12A.

It thus appears that any likely random sequence of environmental changes, even one which for single-age spawners causes a catastrophic decline, can be made to produce instead a large increase in abundance of stock by the simple device of dividing the spawning of each year-class among several calendar years. Even though wholly non-compensatory reproduction cannot occur in nature, this circumstance may have considerable advantage for any population in which random variability is large and/or the left limb of the reproduction curve not very steep (e.g., as in Figs. 1, 2a, 3 or 4). Indeed it is easy to show that in the presence of random variability a multiple-age spawning stock can maintain itself even when its reproduction curve lies wholly below the 45-degree line—though of course it cannot be *too far* below. Thus there is a sound ecological basis for the customary occurrence, in nature, of reproductive assemblages consisting of more than one age-group.

As regards period, we find again that the peaks and troughs of Figure 12A have a certain apparent regularity in spite of their random origin. Discounting the first 15 years as being still somewhat under the influence of the reproduction-curve cycle, and counting all peaks no matter how small, there are 17 peak-to-peak intervals in the figure, of which no less than 10 are of 5 years' duration—the average interval is 5.2 and the range 2 to 7. The fact that the average interval is longer than the 3 which is characteristic of a simple random series (and longer than in the series for single-age spawners) is explained by the method used to obtain it. This is quite similar to taking a "running average" of four items at a time, and Cole (1951, fig. 1) has shown that applying such a procedure to a random series increases the mean peak-to-peak interval. "Artificial" trends of really long period are not as apparent in Figure 12A as in 11A, but a longer series might have confirmed them.

In summary, the characteristics of population changes which would result from density-independent factors acting alone (if that were possible) are as follows:

1. A population of single-age spawners would vary widely above and below its initial abundance; eventually, after a few thousand generations at most, it would either become extinct or, more likely, be fragmented temporarily into small independent units.

2. Populations of multiple-age spawners would increase in abundance indefinitely, though not without ups and downs.

3. The average peak-to-peak period for lines of single-age spawners would be 4.

4. The average peak-to-peak period for multiple-age spawners would be

more than 3, and would be the greater, the greater was the number of ages in the spawning stock; in the example used it was about 5 years.

5. For single-age spawners, and probably for multiple-age spawners as well, "cycles" having longer periods than these would tend to be apparent in graphs of abundance, because of conscious or unconscious mental suppression of small peaks and troughs, and regularization of large ones.

COMBINATIONS OF COMPENSATORY AND NON-COMPENSATORY MORTALITY

In natural populations non-compensatory mortality is superimposed upon the reproduction expected from density-dependent factors, and the curve of population fluctuation is the resultant of both. The random effect can be introduced either before or after the amount of reproduction indicated by the curve is written down, according as the random factors are thought to act before, or after, the compensatory ones. The latter procedure gives greater influence to the random element, and may correspond better to events in nature, though the two types of mortality may of course act concurrently, and to a considerable extent probably do.

Single-Age Spawners

Combinations of Table II or similar series can be made with the various kinds of reproduction curve shown in Figures 1–8. It seems unnecessary to reproduce examples of most of these. With a flat-topped curve such as Figure 2b, and the scale of random variability shown in Table II, the resultant reproduction is practically always equal to the product of the equilibrium abundance and the multiplier or divisor for the year in question. Only an improbably large deviation could shift the population over to the ascending part of the curve for a year. Relatively slight modifications of this situation are obtained when broad-domed curves having a stable equilibrium point are used (e.g., Figs. 3 or 4); the principal difference being that, on the whole, reproduction is somewhat less.

Fluctuations produced by a combination of the reproduction curve of Figure 7 with the random series of Table II have some of the characteristics of either component (Fig. 11). The regular series A–H of Figure 7, repeating at 8-year intervals, is replaced by an irregular one. The average peak-to-peak period is about 3.5—slightly less than that of the random series (which was close to 4) and greater than the 2 of the reproduction-curve sequence. The average amplitude of the "cycles" (ratio of peak to preceding trough) is greater than what either component series exhibits, but there are of course no extreme trends in abundance such as resulted from random causes alone. There is a pronounced tendency for each peak to be followed immediately by a trough, which is a peculiarity also of the random-curve series.

The above description applies whether the random influence operates before the reproduction-curve (Fig. 11C) or after it (Fig. 11B). The two kinds of series are quite similar, but the latter of course has the greater amplitude of changes.

Multiple-Age Spawners

Combination of compensatory and non-compensatory reproduction in multiple-age stocks will be considered only for the case where the former precedes the latter, and will be illustrated by means of a population in which contributions to reproduction are spread over four years in the ratio 2:3:3:2, as in Figure 9.

In general, the kind of fluctuation which results from any combination of compensatory and non-compensatory mortality factors depends upon the relative magnitudes of the two components. The action of the same series of random factors is shown in Figures 12B and 12C at two levels of intensity which are in the ratio of 5:1; Table II is used for B, and values one-fifth as large for C, i.e., 1.36*d*, 1.10, 1.04, etc. In each case they are combined with the reproduction indicated by Figure 7. The same initial age distribution is used for all series of Figure 12.

By itself, Figure 7 yields the steady oscillation of Figure 12D. At the lower intensity of random effects (line C) the population cycle determined by the reproduction curve is not too seriously altered: there is variation in amplitude, and the peaks move out of phase by as much as a fourth at times, yet the prevailing periodicity can be determined fairly accurately from even a short series. At the higher intensity of random effects, however, much greater disturbance is evident; it is followed through in two lines of Figure 12, beginning with B1 and continuing in B2. As regards *period*, the 11-year cycle is first increased to 15–17 years, then reduced to 7 or 8 (counting major peaks only). Though the average over a long period may thus tend to 11 years, peaks and troughs move out of and back into phase with the reproduction-curve cycle and also with the random "cycle", which are its determiners. More serious is the fact that the smaller peaks and troughs of what appears to be the main series are in some cases impossible to distinguish from the "artifacts" resulting from random fluctuation: hence the average 11-year period above could not be discovered in practice, even with a very long record. As regards *amplitude*, the maximum ratio of peak to adjacent trough is much greater than is found in either the reproduction-curve cycle or the random series.

When the random element is given still greater relative importance, the reproduction-curve element becomes unidentifiable as such. However the latter continues to make an important contribution to the resulting population changes. It makes peaks and troughs much less numerous than they would otherwise be, and it provides a control of limits of abundance—that is, the progressive upward tendency of the random curve is effectively curbed.

The relative importance of random and compensatory factors in determining population abundance also depends somewhat upon the number of ages represented in the spawning stock. When this is large, random factors are less effective in disturbing reproduction-curve cycles.

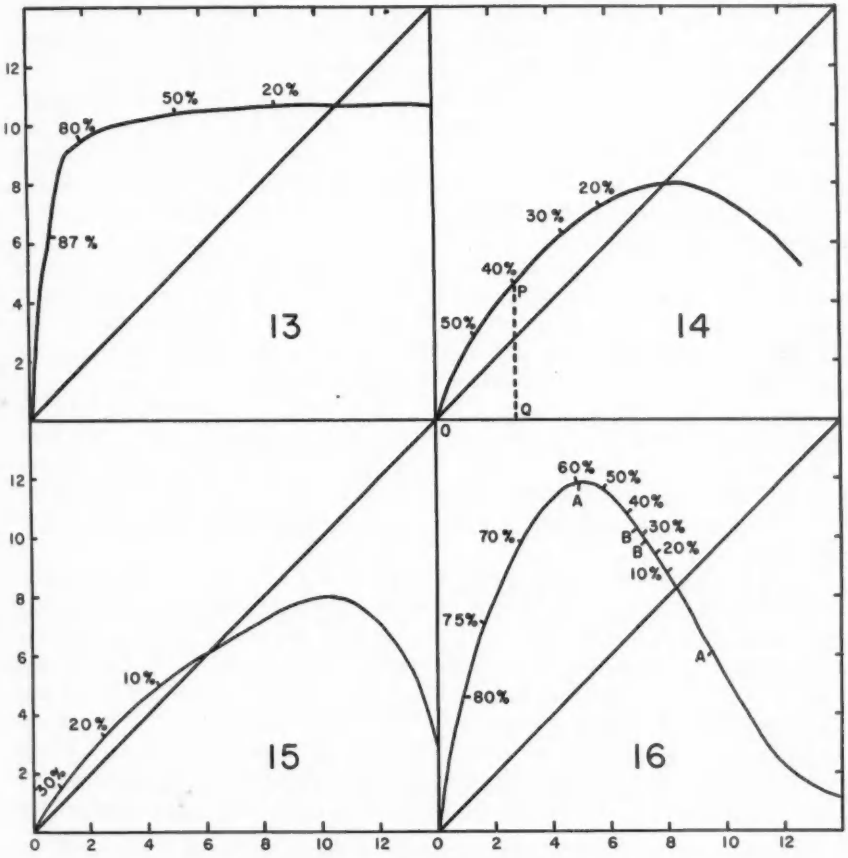
Effects of Removal of Mature Stock

Single-Age Spawning Stocks

Many natural populations have a part of their members removed by man, either because they are useful to him or, in the case of harmful species, because

he hopes to reduce their abundance. The case where only *mature* stock is taken by the fishery is considered in examples to follow. Many fisheries take a portion of the immature stock also, but this appears not to add any new principle to what is considered below, provided the region of compensatory mortality is not invaded.

The effect upon the various population parameters of removing a constant percentage of the mature stock, before reproduction, is shown for four types of single-age-group populations in Figures 13–16. In Figure 14, for example, a spawning stock OQ produces filial spawners equal to PQ. However, after the fishery has removed 40 per cent of the mature stock the number remaining is equal to OQ, which again produces PQ, and so on. Thus P is the equilibrium position for 40 per cent



FIGURES 13–16. Equilibrium densities of stock for the various rates of exploitation indicated by percentages on the reproduction curve. Stock density before fishing is the ordinate value corresponding to the point on the curve opposite the percentage exploitation in question. Axes as in Figures 1–4.

exploitation. The fraction of the mature stock which must be removed prior to spawning, in order to maintain equilibrium at any point on the reproduction curve, is equal to the complement of the reciprocal of the slope of a line joining that point to the origin.

The general effect of exploitation is to move the point of equilibrium abundance to the left on the reproduction curve. In Figures 13–15 this means that under exploitation the equilibrium population is always smaller than it is under natural conditions. In Figure 16 (which is the same as 7), removal of part of the spawning stock at first results in a *larger* equilibrium level of stock, and the same is true of Figures 5, 6 and 8. When rate of exploitation becomes large enough, however, the stock is again reduced. Equilibrium points for various rates of exploitation are indicated on Figures 13–16.

Oscillating equilibria are much changed by exploitation. Their amplitude is reduced, and the number of positions through which they swing is decreased, or oscillation may be eliminated entirely. However, stable oscillations persist when exploitation is light to moderate. In Figure 16, for example, with 10 per cent removal the stock traces the cycle 11.9, 4.0, 10.9, 5.5, 11.9, etc.; with 20 per cent removal it alternates between the levels of 6.1 and 11.9 units (A–A); with 30 per cent removal the oscillation is reduced to between 9.9 and 10.3 (B–B), so that it would not be distinguishable in practice; and with 60 per cent removal it disappears completely[6].

The point of maximum sustained yield can easily be computed from graphs like Figures 13–16. For example, in Figure 16 it is at 65 per cent exploitation; in Figure 13 it is close to 80 per cent; in 15 only about 18 per cent. In general, the greater the area between the reproduction curve and the 45-degree line above the latter, the greater is the optimum rate of exploitation.

Beyond the level of maximum yield lies a level of maximum permissible exploitation above which the stock is progressively reduced to zero. This limit is a function of the maximum angle made by any line joining a point on the reproduction curve to the origin; and as noted above, the maximum rate of removal which can be sustained is equal to the complement of the cotangent of that angle.

If a man's interest in a single-age population, of a noxious insect for example, is to reduce it to as low a level as possible by increasingly intensive destruction, he can be sure of making *direct* progress toward the desired goal only if the reproduction curve is one of the types shown in Figures 1 and 2. If it is like Figures 3 or 4, and stock happened to be on the outer limb, some moderate rate of removal would dampen a crash which otherwise was imminent. With curves of types 5–8 a paradoxical situation develops. Moderate destruction of adults will in general tend to stabilize the population at or about some magnitude *greater* than its primitive average abundance. In Figure 16 maximum abundance is con-

[6]When equilibrium is unstable the *average* size of the populations of the cycle tends to be less than the equilibrium level. In Figure 16 the average is 7.7 for no exploitation, 7.8 for 10 per cent, and 9.0 for 20 per cent, as compared with the equilibrium values of 8.2, 8.6 and 9.4. For 30 per cent or greater exploitation, equilibrium stock and average stock are the same.

sistently achieved when as much as 60 per cent of the spawning stock is destroyed each year. To reduce the population below the primitive average, more than 73 per cent must be destroyed. Thus although sufficiently intensive effort will be successful, moderate destruction of the mature population is worse than no action at all[7]. Furthermore, if an intensive campaign of continuing control of a variable species is decided upon, it is most efficient to begin it at a time that the population is at a low point of its cycle, i.e., when the pest may be doing no particular damage.

Multiple-Age Spawning Stocks

The effect of a fishery upon stocks containing more than one age-group of spawners parallels what has just been found for single-age-group stocks. If the stock is one for which a stable equilibrium exists (Figs. 1–5), adding a fishery does not disturb the stability, but the abundance of the population is changed (in 2b the change begins only after the inflection point is reached). With the curves of Figures 1–4 the change is in the direction of a decrease in abundance, but with Figure 5 exploitation at a moderate rate *increases* the adult stock, until the dome of the reproduction curve is reached.

Stocks which perform regular oscillations in the absence of a fishery (Figs. 7 and 8) are changed in three respects when exploitation begins: (1) their average equilibrium abundance is at first increased, but later decreases again if exploitation becomes sufficiently intensive; (2) the amplitude of oscillation decreases; and (3) the period of oscillation tends to decrease slightly.

1. The first-named effect can be estimated rather easily, since the average abundance of multiple-age stocks proves to be practically the same as the equilibrium abundance. The latter has been calculated for Figure 16 using various rates of exploitation, as shown on that Figure and in Table III. The maximum abundance is at the dome of the curve, and maximum catch is obtained slightly to the left of it, at 65 per cent exploitation.

2. The advent of fishing not only affects the total abundance of a stock, but also gives it a younger age composition, because survival rate from year to year is reduced. In the example of Table IV, based upon Figure 16, the fish are assumed to mature first at age III. Fishing takes place just prior to spawning and rate of fishing is the same for all ages. Natural mortality occurs between successive fishing-and-spawning seasons, and is 20 per cent from age III to age IV, 20 per cent from IV to V, 30 per cent from V to VI, and 100 per cent after the spawning at age VI. The average weight of a fish at time of fishing-and-spawning is 2 units at age III, 4.28 units at IV, 7.14 at V and 9.52 at VI; and egg production is proportional to weight. Under these conditions the *equilibrium* distribution of the contributions of the several age-groups to egg production, at different rates of exploitation, is shown in Table IV.

[7]A similar conclusion is reached in Nicholson and Bailey's (1935) detailed analysis of host-parasite interaction in insects. Varley (1947) concluded that a trypetid fly population was maintained at about 10 times the density it would otherwise have had, because of the presence of non-compensatory causes of mortality which killed host and parasite equally.

TABLE III. Average or equilibrium abundance of stock, by weight, in a stock having more than one age at maturity, and the catches at various rates of exploitation; from Figure 16.

Rate of exploitation	Stock before fishing	Catch
%		
0	8.2	0
10	8.8	0.9
20	9.5	1.9
30	10.1	3.0
40	10.8	4.3
50	11.5	5.8
60	11.9	7.1
65	11.4	7.4
70	9.7	6.8
75	7.2	5.4
80	5.0	4.0

TABLE IV. Relative weights and contributions to reproduction of the age-groups in the stock described on page 583.

Rate of exploitation	Fraction of eggs contributed by age			
	III	IV	V	VI
%				
0	0.200	0.300	0.300	0.200
10	0.233	0.314	0.283	0.170
20	0.273	0.327	0.261	0.139
30	0.320	0.336	0.235	0.109
40	0.377	0.339	0.204	0.081
50	0.446	0.333	0.165	0.055
60	0.526	0.315	0.127	0.032
70	0.619	0.278	0.083	0.020
80	0.737	0.221	0.042	0.000

The first line of Table IV was arranged to have the same distribution of contributions to spawning as used for Figure 9F. In Figure 17 are shown cycles obtained from the 10 per cent and 20 per cent lines of Table IV, starting from the equilibrium distribution characteristic of no fishery[8]. At 10 per cent exploitation the oscillation of the population is maintained, though at reduced amplitude and about a higher mean level. At 20 per cent exploitation oscillation gradually decreases to an inconsiderable amplitude, and at higher rates of exploitation it

[8]This procedure is the only practicable one, but it ignores the fact that the age distributions of Table IV would themselves be completely realized only after a period of 4 years from the beginning of fishing. Consequently the equilibrium situations in Figure 17 would actually be approached more gradually than the figure indicates.

disappears completely. However even at 20 to 40 per cent exploitation the oscillation persists through several cycles.

3. The length of a cycle was found earlier to be twice the mean length of a generation (interval from egg to egg). In the first line of Table IV this is 4½ years, and the cycle is 9 years. With the higher exploitations of Table IV a shift of age distribution toward younger fish occurs, and we accordingly expect

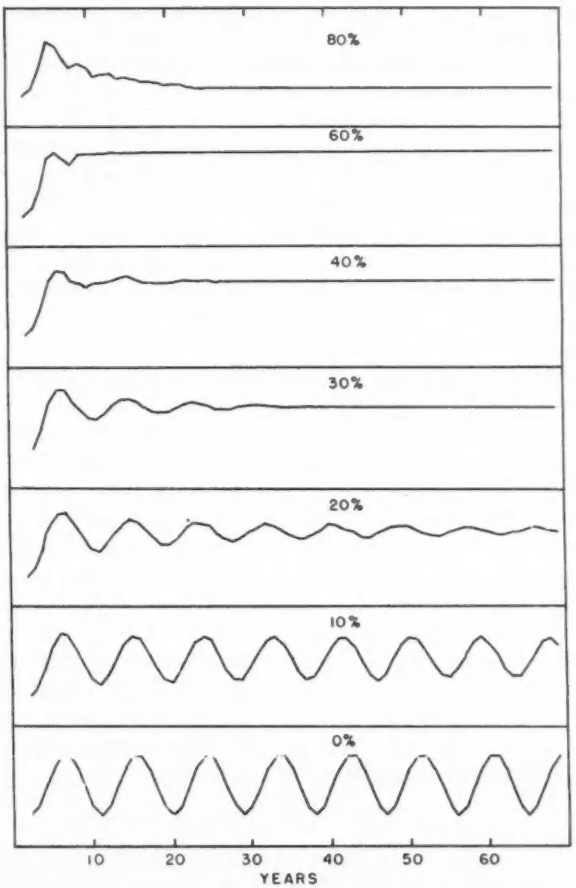


FIGURE 17. Reactions of an hypothetical population to exploitation. The population is one regulated by the reproduction curve of Figure 7, with ages III, IV, V and VI contributing to egg production in the ratio 2:3:3:2 when there is no exploitation. The stable cycle characteristic of no exploitation is shown by the 0% line. The other lines show the effect of annual removal of the indicated percentage of the mature stock from a population which initially had the age distribution characteristic of the start of the ascending phase of the no-exploitation cycle. (See also footnote 8.)

a shorter cycle to appear. In this example, however, the cycles disappear before much decrease in period can take place. At 10 per cent exploitation average age of contribution to reproduction is reduced to only 4.39, and at 20 per cent it is 4.27. The corresponding predicted cycle lengths are 8.8 and 8.5 years, and the peaks shown in Figure 17 do in fact become progressively a little closer together. In a somewhat more realistic example there would have been more than four age-groups in the stock under conditions of light exploitation or none, and in that event the reduction in period of oscillation with increased fishing would be greater. However it is doubtful whether in nature the reduction would ever be great enough to be identifiable with certainty, before increasing exploitation removed oscillation of this type entirely.

When the reproduction curve is dome-shaped, *control* of an undesirable population of multiple-age spawners presents some of the same difficulties as described earlier for single-age stocks. However the initial favourable reduction in abundance will tend to last longer—i.e., until the increased broods of young can grow to the size at which they cause damage. Only when this first phase is over, and the fishing effort has to cope with the larger broods which come from the reduced spawning populations, will it be apparent whether or not control can be permanently effective. Few recorded attempts to reduce nuisance fishes have lasted beyond the initial stage of removal of old stock. Foerster and Ricker (1941) have described the rather easy success achieved in this preliminary phase of control of squawfish (*Ptychocheilus*) in a small lake. The experiment was subsequently continued until one or more large broods of young began to grow into the damaging size range, but it did not last long enough to see if these could be kept sufficiently reduced by appropriate effort. In Lesser Slave Lake, Alberta, unlimited fishing for ciscoes began in 1941 with the hope of thus reducing the lake's population of the tapeworm *Triaenophorus*, and as a result the spawning population has been changed gradually from one 5–7 years old to one now (1951) mostly 2 years old. However recruitment and rate of growth have increased sufficiently to maintain a high level of catch and a fairly large population mass, so that control is not yet effective for the purpose intended (Miller, 1950, 1952).

When non-compensatory variability is added to the effects of exploitation and the reproduction curve, the kind of result obtained differs little from what was discovered from Figure 11. The amount of disturbance introduced depends of course upon the relative magnitude of the random factors.

EXAMPLES OF REPRODUCTION CURVES

A wider recognition of the different possible kinds of reproduction curves, and their different properties, will be of value mainly as a guide to current and future research. Such curves should be useful not only as a possible clue to the nature of observed fluctuations, but still more in estimating expected average recruitment when stock is reduced (or increased!) by fishing it, at different intensities. Knowledge of the reproduction curve will thus complement information on rate of growth and natural mortality, and permit more accurate prediction and regulation of fish catches.

Some examples are given below of reproduction curves, for fish and a few other animals, which can be plotted from available data. In several instances information is available concerning only the first part of the life history, but since that is where most compensatory mortality is expected, the data are included. A disadvantage of such curves, however, is that the "45-degree line" can usually be located only approximately, if at all.

PACIFIC HERRING (*Clupea pallasi*)

The herring of the west coast of Vancouver Island are a natural unit which has been given special study. Recently Tester (1948) examined the relation between the intensity of spawning in the brood year, and an estimate of resulting year-class strength based on catch per unit effort in the various years that each brood contributes to the fishery. Tester had two indices of spawning; using "Index A", which was available for five years longer than "Index B", he computed an inverse correlation of —0.30 between spawn deposited and resulting year-class strength for the period 1931–43, though this figure does not differ significantly from zero.

Mr. J. C. Stevenson has very kindly added data for more recent years, and these are plotted in Figure 18. In this figure the more elaborate "Index B" is used, but the five years 1931–34 are included (open circles) using values from the regression of B on A for the years of overlap. The negative correlation —0.16, for the years 1931–49, differs from zero even less than the one computed by Tester, principally because a series of abundant year-classes from 1943 to 1947 has increased the range of variability. However it is still true that the largest

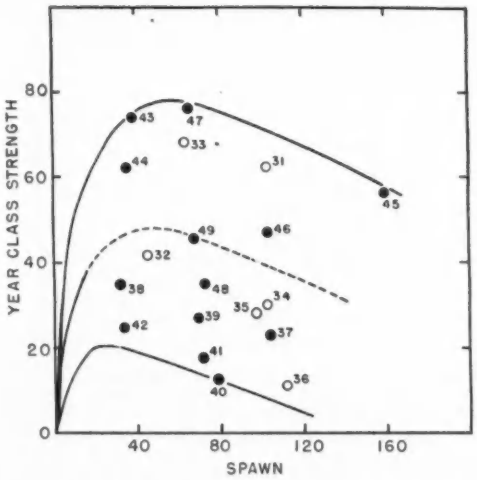


FIGURE 18. Relative strength of year-classes of a Pacific herring stock (ordinate) plotted against relative amount of spawn deposited in the brood year (abscissa). The two solid lines include the observed limits of variation, while the dotted one is an approximate middle value. Data from Tester (1948) and Stevenson (MS).

broods have been produced by smaller-than-average spawnings, whereas the smallest broods have been produced by larger-than-average spawnings.

Dr. Tester and others have also considered the possibility that trends in herring recruitment may exist corresponding to some as yet unidentified rhythm of the ocean environment; and the 1943–47 stanza of good year-classes is in fact fairly well set off from earlier (1934–42) and later (1948–49) stanzas of lower production (Fig. 18). If there is really any systematic effect here, one may notice that *within* each of the two longer stanzas a negative correlation between spawning and recruitment is indicated.

PINK SALMON (*Oncorhynchus gorbuscha*)

Among pink salmon there are two completely separate reproductive lines[9], so that is is very easy to identify the progeny of any year's spawning when it matures two years later. From Pritchard's (1948a, b) summary of the reproduction of the stock which spawns in McClinton Creek, Graham Island, British Columbia,

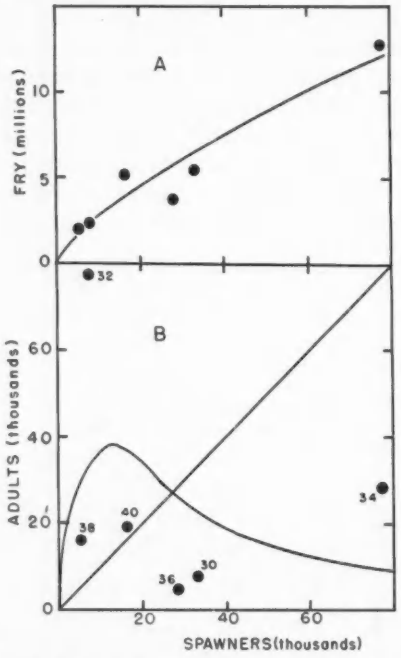


FIGURE 19. A—Fry produced in millions; and B—returning adults in thousands; plotted against the number of pink salmon spawners in the brood years indicated, at McClinton Creek, B.C. Data from Pritchard (1948a, b).

[9]Separate or nearly separate breeding stocks of salmon are commonly called "cycles", "years" or even "races" in western North America. The term "lines" was proposed by Huntsman (1931), and is used here because it avoids confusion with other kinds of cycles, etc. (cf. Clemens, 1952).

the reproduction curve of Figure 19B is plotted. The progeny shown does not include the commercial catch, which is a considerable but unknown quantity, and hence all points would be moved upward on a graph that represented total adult production of the spawnings indicated. No very clear idea of the shape of the reproduction curve can be obtained, but it seems to slope downward from 15–20 thousand spawners.

Dr. Pritchard also had records of fry production, and these are plotted in Figure 19A. The fact that *percentage* fry production decreases as population increases indicates that compensatory mortality occurs in the freshwater part of the life history. That compensation occurs also during saltwater life is suggested by the change from a generally upward slope in Figure 19A to a generally downward slope in 19B. Obviously too there is much random variation in mortality at both stages, but particularly in the ocean. The ocean phase includes the effect of exploitation by the fishery, which is certainly variable and might tend to be

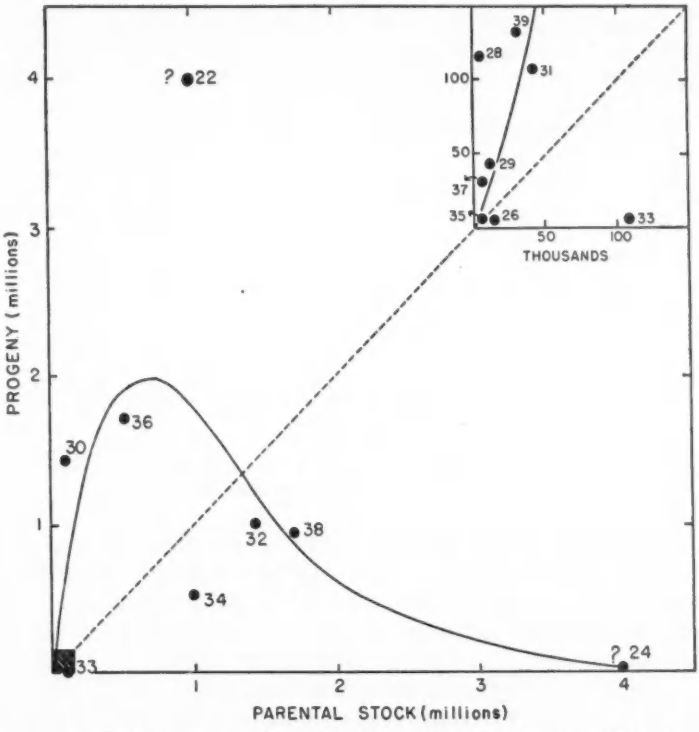


FIGURE 20. Reproduction curve for pink salmon of the Karluk River, Alaska, based upon fence counts except in 1922 and 1924 (see text). The shaded square in lower left is shown on a larger scale in the upper right corner. Commercial catches are not included in the progeny. (From unpublished data of the United States Fish and Wildlife Service, Pacific Salmon Investigations.)

compensatory, because more seiners are attracted to the bay off McClinton Creek when fish are numerous there.

A reproduction curve having a very wide range of parent-stock densities is that for pink salmon of the Karluk River, Alaska. This is shown in Figure 20, plotted from data supplied by Messrs. C. E. Atkinson and C. J. Burner of the U. S. Fish and Wildlife Service. "Progeny" figures do not include the commercial catch; adding the latter could not alter the general form of the curve, but would raise it farther above the 45-degree line. The 1926–40 data are from complete or nearly-complete fence counts. The 1924 escapement was estimated as "over 4,000,000" (Barnaby, 1944, p. 257). Unfortunately there is no numerical estimate of the 1922 run; however, since it is called "large" on the same page as the 1924 run is called "tremendous" (Barnaby, p. 249), it might be assigned a figure of about one million, and on that basis a point for 1922 is plotted in order to better indicate the vertical range of reproduction.

Coho Salmon (*Oncorhynchus kisutch*)

The experiment at Minter Creek, near Tacoma, Washington, has provided information on the relation of spawning stock to smolt output (Smoker, 1954). Production of year-old smolts is related to number of female spawners in Figure

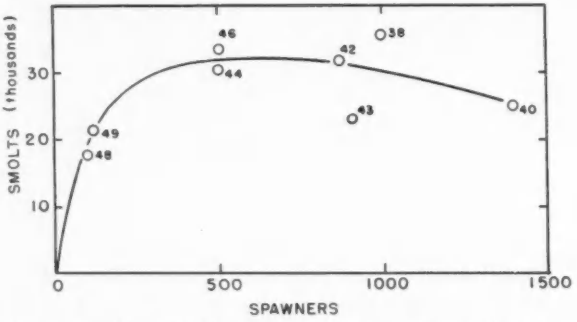


Figure 21. Smolts produced by adult female coho salmon spawners of the brood years indicated, at Minter Creek, Washington. Data from Smoker (1954).

21, based on the same data as the upper half of Smoker's figure 29. The productive capacity of the stream appears to be 25–35 thousand smolts, depending mainly on volume of flow (Smoker's fig. 29, lower half), and if adjustment is made for the latter, the already-flat outer limb of Figure 21 becomes even flatter, with the deviations of the points from the line considerably reduced.

Estimates of total adult production from these smolts are not possible; there is no record of catch, and even the number of returning spawners is available for only four years.

Sockeye Salmon (*Oncorhynchus nerka*)

The sockeye of Karluk Lake, Alaska, mature at 3 to 8 years of age, the mean being a little over 5 years. Barnaby (1944, fig. 3) has plotted a graph of spawning

stock against adult progeny produced; the latter was obtained by summing the contributions of the 1921–29 year-classes to subsequent catches and breeding stocks. This graph is practically equivalent to a reproduction curve based upon eggs, the only difference being that possible variation in the number of eggs produced by females of different ages is not taken into account.

Barnaby separates "spring" and "fall" fish in his plotting. Either in this form, or when the data for each year are combined (Fig. 22), there is much variability in production, but a peak apparently occurred when the total spawning stock (spring plus fall) was between 1 and 1½ million fish. Unfortunately, both before and after this period the sockeye stock of the lake decreased, so the 1921–29 results cannot apply either to the earlier period when *catches* of 2–3.5 million fish were customary, or to the modern period when the total stock has fallen below a million. The causes of this decrease are still under study.

An opportunity to document the *ascending* phase of a sockeye reproduction curve is afforded by the "late Shuswap" or Adams River race on the Fraser River. A blockade in 1913 reduced this and other Upper Fraser races of sockeye to a level that was only a small fraction of their natural abundance. These fish mature preponderantly at 4 years of age, so that an adequate reproduction curve

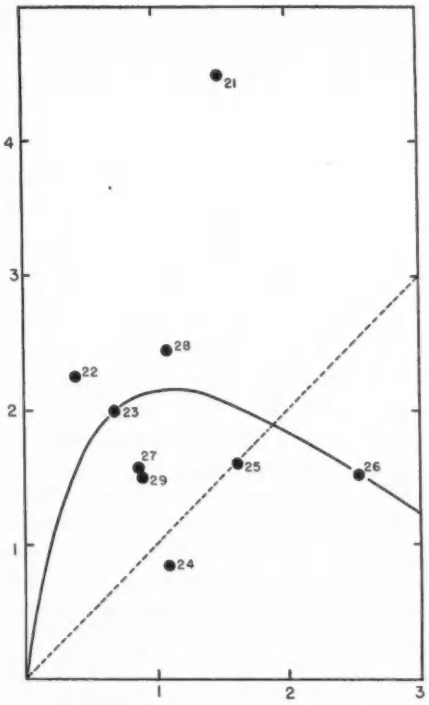


FIGURE 22. Number of mature sockeye (catch plus escapement) produced by the year-classes of 1921–29, at Karluk Lake, Alaska. Data from Barnaby (1944).

can be plotted using estimates of spawners and catches every fourth year (Fig. 23). Sizes of the spawning population are based on estimates of Fishery Inspectors and, in recent years, on figures given in Annual Reports of the International Pacific Salmon Fisheries Commission; the catch is taken as the total Fraser commercial catch each year, less 1,200,000 fish representing the approximate production of other races in this series of years. The curve has a much steeper ascending limb than the Karluk curve; there is a suggestion of a maximum at 1–1.5 million spawners, and possibly a start on the downward path beyond that point.

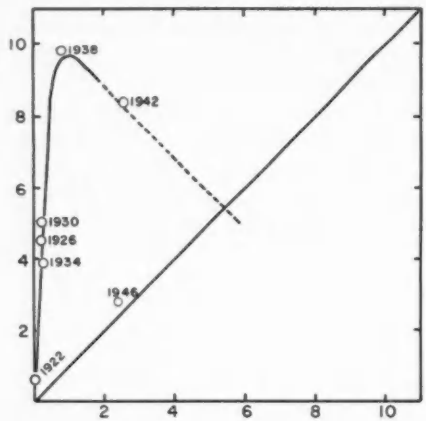


FIGURE 23. Reproduction curve for the late Shuswap race of sockeye salmon, based upon estimated numbers of spawners and an approximate division of the commercial pack. *Abscissa*—estimated number of spawners in the years indicated; *ordinate*—resulting catch plus escapement. Both scales are in millions of fish. The year of spawning is shown beside each point. From data of the B.C. Department of Fisheries and the International Pacific Salmon Fisheries Commission.

The steepness of the left limb of the Shuswap curve is worth noting, being of the same order as that of Figure 8. If the right limb has any considerable slope downward, it would have a tendency to mould chance fluctuations into swings back and forth across the 45-degree line. In this connexion one may note that the original dominant line of sockeye on the Fraser, of which the late Shuswap race was a component, is supposed to have been considerably less abundant in 1909 than in either 1905 or 1913 (Babcock, 1914). This might represent two swings across an equilibrium position, under the then conditions of a fairly low percentage exploitation of this line by the fishery (compare A–A of Fig. 16). Under present conditions the fishery normally takes enough to keep the spawning stock near the dome of the curve, and special measures are taken to ensure this much escapement when below-normal reproduction has occurred, as from the 1946 spawning (Royal, 1953).

HADDOCK (*Melanogrammus aeglifinus*)

Herrington's (1941, etc.) analysis of the George's Bank population is particularly valuable because he was able to obtain from market reports an estimate of the smallest commercial size (scrod—mostly age III) independently of and in addition to the larger sizes. This yields an estimate of recruitment from year to year, which in turn is a reflection of success of reproduction. When size of spawning stock in the years 1912 to 1929 is plotted against scrod produced (solid circles, Fig. 24), a steep outer limb of a recruitment curve is apparent. The 45-degree line has been located very approximately by considering that a pound of scrod during those years had an expectation of egg production, throughout its life, equivalent to the actual egg production in one year of 10 pounds of mature haddock; and by assuming that scrod were half as vulnerable as were adult fish

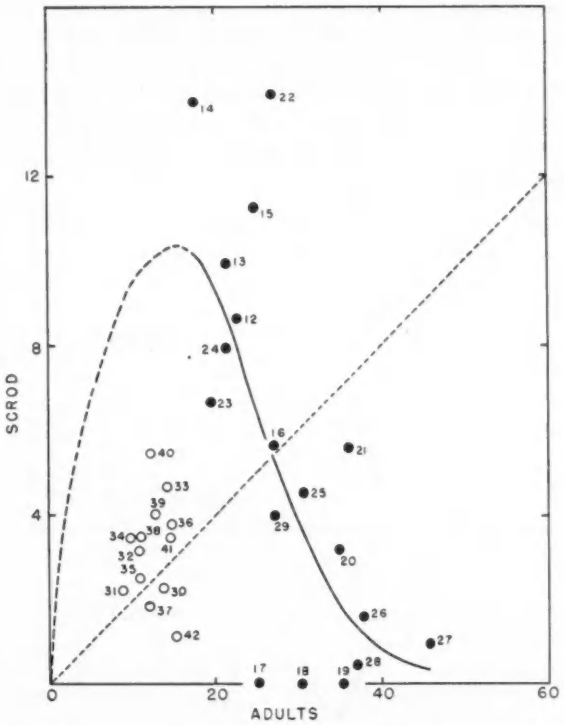


FIGURE 24. Abundance of adult haddock on George's Bank during spawning season (February–April), related to abundance of scrod (age III, mostly) at the same season three years later. Both scales are in terms of thousands of pounds per day caught by trawlers of a certain size class, the figures for adults being smoothed. Black circles represent the years 1912–29, open circles 1930–43. The reproduction curve is drawn for the earlier period only. The diagonal is an *approximate* 45-degree line for that period (see text). Data from Herrington (1948).

to the trawlers whose catches supply these data. Figure 24 is the same as Herrington's figure 11 of 1948, except that we have used catches of the February-April period only, for both scrod and adults. Herrington was of the opinion that the critical time for competition between adults and young, during those years, was when the young were about a year old (his fig. 12); however the two graphs are much the same and do not provide a basis for decision on this point. Either one supports Herrington's interpretation of the fluctuations in adult stock over the period in question, which consisted of two complete oscillations (Fig. 25). The trough-to-trough periods were 9 and 8 years, and trough:peak amplitude was about 1:2. The observed period implies a median age of 4 or 5 years for the production of eggs by the fish of each brood, and this seems consistent with what is known of the size- and probable age-structure of the haddock population in those years.

Thus Herrington has described the only example yet known in which oscillation of a multiple-spawning-age fish population might plausibly be ascribed to the simple effect of a steep reproduction curve. His account of the probable cause of the inverse stock-recruitment relationship emphasizes competition for food between adults and young. Intra-brood competition at an earlier age seems another possible factor, but the feeding habits of haddock are said to preclude significant cannibalism.

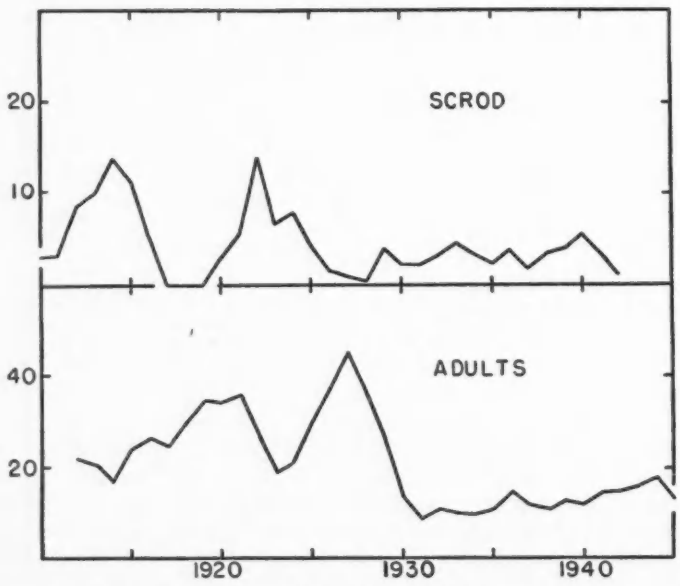


FIGURE 25. Catch per unit effort of adult haddock, related to that of the scrod (age-III fish) produced by them. The years shown on the abscissa are those in which the adult catch was made; the scrod on the same ordinate were taken three years later. From the same data as Figure 24.

Points for the years 1930–43 are plotted as open circles in Figure 24. About 1930 the haddock fishery changed radically within a few years; total effort increased, and otter trawls to a large extent superseded baited-hook methods so that smaller fish became relatively more intensively exploited. Although adjustments for these effects were made as well as possible by Herrington, quantitative comparisons between the period before and after 1930 appear uncertain. In particular, the relative level of recruitment indicated after 1930 seems too low to have sustained the continuing fairly high level of catch—that is, the 45-degree line indicated on Figure 24 probably does not apply to these later years.

What is of most interest for us is that the increase in rate of exploitation about 1930 was sufficient to eliminate oscillation from the population (Fig. 25). It was discovered in Figure 17 above that, in a stock subjected to increasingly heavy fishing, reproduction-curve oscillation may disappear while rate of exploitation is still rather low; and further, that the transition from marked oscillation to unrecognizably small oscillation occurs rather abruptly. Possibly accidental, but also in accord with expectation in a fishery of increasing intensity, is the fact that the second cycle in Figure 25 is shorter than the first (*two* years shorter in Herrington's representation).

Fruit Fly (*Drosophila melanogaster*)

An optimum population density for reproduction was found by R. Pearl and S. Parker in a series of experiments made during the early 1920's. The reproduction curve of Figure 26A is synthesized from graphs summarizing their work, given by Lotka (1925).

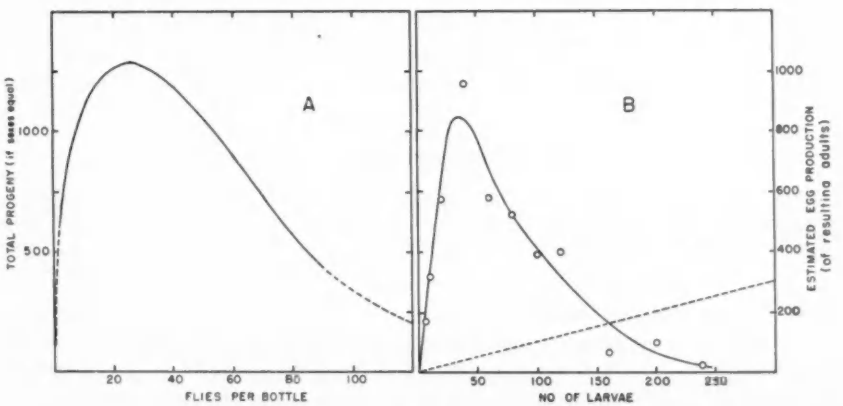


Figure 26. Reproduction curves for *Drosophila melanogaster*. A—From data of Pearl and Parker, as presented by Lotka (1925). The ordinate represents half the product of the density in question, times the progeny produced per female per day, times the mean length of life. The range over which observations were actually made is shown as a solid line. B—From data of Chiang and Hodson (1950, table 9 and fig. 13). The abscissa is the number of 24-hour larvae used to start a culture, and the ordinate is the potential egg deposition of the resulting adults. The dotted line is an approximation to the 45-degree line, which ignores possible mortality in the egg to 24-hour larva stages.

Recently Chiang and Hodson (1950) have investigated *Drosophila* reproduction in more detail. Figure 26B shows their graph of "potential fecundity" against initial larval density. Some of the factors involved in decreasing the reproduction with increasing density were greater larval mortality, increased failure to pupate, and smaller size and lesser fecundity of adults produced. The flattening of the curve near the right end was due partly to a secondary *increase* in pupal and adult size at the highest densities.

Azuki Bean Weevil (*Callosobruchus chinensis*)

Extensive studies of this species have been made by S. Utida, but the only account I have been able to consult is that of Fujita and Utida (1953). There is no overlapping of generations. A reproduction curve is shown in Figure 27, obtained under experimental conditions. The right limb trends downward with a slope numerically less than unity, which would make the population subject to damped oscillations. Such oscillations were actually observed by Utida (Fujita and Utida, p. 494).

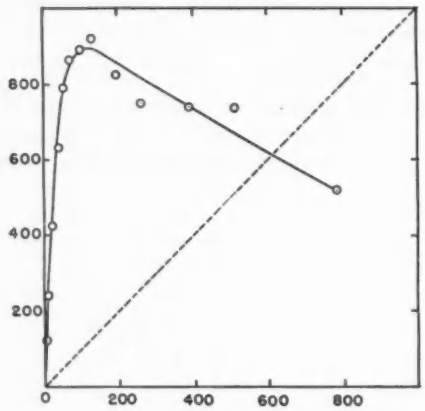


Figure 27. Reproduction curve for the azuki bean weevil under experimental conditions. *Abscissa*–size of parental generation; *ordinate*–number of mature progeny. Replotted from figure 4 of Fujita and Utida (1953).

Water-Flea (*Daphnia magna*)

Pratt (1943) performed experiments on the effect of stock density upon the production of young and upon longevity, in *Daphnia* grown in 50 cc. of culture medium with excess food. These can be used to construct reproduction curves, shown in Figure 28.

The ordinates in Figure 28 are equivalent to the total number of young produced in an average lifetime at the temperature and density in question (Pratt, p. 135). The identity of these values with those required for a reproduction curve can be shown as follows. Consider the life of a *Daphnia* to be divided into a series of "generations", corresponding to the years of an ordinary fish's life. These could be made of any length, but for convenience they are taken as equal to the approximate time from hatching to first maturity (6 days at 25°C., 14 days

at 18°C.). Then consider a 10-*Daphnia* population at 25°. It produces young which live 26 days on the average (Pratt's fig. 6), or 4.3 "generations". During the first of these the *Daphnia* are immature, so that their mature life is 3.3 "generations". The total young produced by an individual in an average lifetime is, however, 23.1 (Pratt, p. 135), or 7.0 per generation. Consequently a population of 10 mature individuals produces $10 \times 7.0 = 70$ young per "generation", and these survive through 3.3 generations of maturity on the average, so that the total reproductive potential produced by the parent generation is $70 \times 3.3 = 231$ units. These "units" are numerically the same as the total number of young which would be produced throughout the life of the 10 parent individuals living at constant density. However the "units" are to be regarded not as young actually produced, but as a measure of the generation's potential contribution to the mature population of several future generations, in exactly the same way as eggs in mature females were used for fishes. In actuality, if stock density were to change by the time these 231 "units" were in the mature population, the actual production of young by the progeny of the original generation would be greater or less than 231.

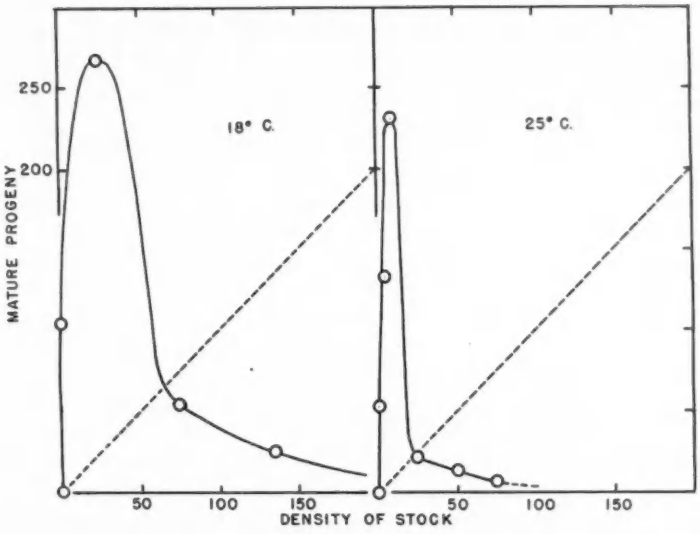


FIGURE 28. Relation between density of adult *Daphnia magna* and their expectation of progeny, at 18° and 25°C. Computed from data of Pratt (1943): 18° curve from his figs. 7 and 8; 25° curve from his figs. 5 and 7.

The reproduction curves of Figure 28 are of a steeper type than any of those discovered among fishes, particularly the 25° curve. Both curves are in fact likely to be even steeper than they are drawn, since the highest point of observed production of young is not necessarily the maximum. This steepness has been believed to be associated with the small volume of habitat and consequent likelihood of waste accumulation—although the medium was changed every second day.

Pratt (1943, figs. 1, 2) also followed the growth of *Daphnia* populations over a period of 6–7 months under the same culture conditions as outlined above. Starting in each case from 2 parthenogenetic females not more than a day old,

TABLE V. Simplified calculation of ideal population changes of *Daphnia magna* at 25°C. under the conditions of Pratt's experiments, by 6-day periods. Average mortality is considered as zero for the juvenile 6 days, one-fourth from the first to the second 6 days of maturity, one-third from the second to third, one-half from the third to fourth, and 100 per cent after the fourth. The number of "reproductive units" produced by a given stock in 6 days is defined as the product of the number of mature animals produced times the average number of 6-day periods each lives. Column 6 shows the total units produced by the stock of column 5, values being taken from Figure 29B. These units are divided among the appropriate periods to give the stock present, as shown in the first four columns. The population starts as two newly mature adults, one of which survives for two 6-day periods, the other for four. Total adult stock thereafter is the horizontal sum of the units in the first four columns. The total stock (column 7) is the adult stock (column 5) plus the number of juveniles, the latter being the same as the initial number of matures, as indicated in column 1 one 6-day period later.

1	2	3	4	5	6	7	1	2	3	4	5	6	7
Fraction mature during successive 6-day intervals				Adult stock	Reproductive units produced	Total stock	Fraction mature during successive 6-day intervals				Adult stock	Reproductive units produced	Total stock
0.4	0.3	0.2	0.1				0.4	0.3	0.2	0.1			
..	..	..	..	2	65	2	6	2	1	0	9	230	101
..	..	..	..	2	65	28	92	4	1	0	97	4	189
26	..	..	..	27	20	53	92	69	3	0	164	4	166
26	20	..	..	47	15	55	2	69	46	2	119	4	121
8	20	13	..	41	15	47	2	1	46	23	72	6	74
6	6	13	6	31	20	37	2	1	1	23	27	20	30
6	4	4	6	20	40	28	3	1	1	0	5	160	13
8	4	3	2	17	90	33	8	2	1	0	11	230	75
16	6	3	2	27	20	63	64	6	1	0	71	6	163
36	12	4	2	54	10	62	92	48	4	0	144	4	147
8	27	8	2	45	15	49	3	69	32	2	106	4	108
4	6	18	4	32	15	38	2	2	46	16	66	6	68
6	3	4	9	22	25	28	2	1	1	23	27	20	30
6	4	2	2	14	200	24	3	1	1	0	5	160	13
10	4	3	1	18	65	98	8	2	1	0	11	230	75
80	8	3	2	93	4	119	64	6	1	0	71	6	163
26	60	5	2	93	4	95	92	48	4	0	144	4	147
2	20	40	2	64	6	66	3	69	32	2	106	4	108
2	1	13	20	36	15	39	2	2	46	16	66	6	68
3	1	1	6	11	230	17	2	1	1	23	27	20	30

the 18° cultures rose to a peak of about 200 animals usually after about 70 days, decreased to about 120 animals, then showed a slight increase. At 25° the cultures grew more rapidly, reached a peak in 20 days, and then as rapidly declined; sometimes they died out, but in two instances the oscillation was repeated four times before the experiment terminated. Figure 29 shows one example at each temperature.

The steep reproduction curves of Figure 28 immediately suggest the possibility of oscillations, and they have been used to obtain the computed population curves (B and D) of Figure 29. These start from 2 newborn animals, like Pratt's figures 1 and 2.

Construction of the curves of Figure 29 required certain assumptions and simplifications. The life of a *Daphnia* was divided into "generations" as before. The total number of "reproductive-units" indicated by the ordinate of Figure 28 was divided among successive generation-long periods of life as follows: for 25°C., in the ratio 0:4:3:2:1; for 18°C., in the ratio 0:22:20:18:14:11:9:5:1. These ratios correspond approximately to the average survival indicated by Pratt's figures 5 and 8. The calculation then proceeded on the same basis as in Table I, the sequence for 25° being shown in Table V. Because Pratt's censuses include immature individuals, the mature stock of column 5 is increased by the number of immatures in the culture (considered equal to the first generation of matures, in column 1 one line below) to give the total stock of column 7.

Obviously this computation differs from actuality in the assumption of an age distribution of mortality that is independent of density (cf. Pratt's figs. 5 and 8). The difference is most serious at 25°, and if a more complex calculation were made to take account of it, the initial effect would be to make the troughs deeper because of the shorter lives of denser stocks.

The predicted course of events in Figure 29 has considerable resemblance to what was actually observed in respect to period, and to a less extent in amplitude. (Pratt's observed curves also vary a lot among themselves, as would be expected when the stock starts out from, and at 25° is periodically reduced to, a very few individuals.) Any judgment concerning the significance of this resemblance would have to be of the subjective type which Smith (1952) rightly deplores, but the comparison has the merit that the factual bases of the two curves of each pair are from different sources—there are no "fitted constants".

At 18° the computed cycles are soon damped to an inconsiderable amplitude, but the suggestion of a second low peak in the observed series (Fig. 29A) would probably have been confirmed if the cultures had been maintained a month or so longer. At 25° the computed oscillation reached a stable equilibrium pattern having a large amplitude by the time of the fifth peak, and the two surviving observed series were still oscillating strongly when they were discontinued. The striking difference between 18° and 25°, in both the calculated and the observed curves, is ascribable partly to the steeper reproduction curve at 25°, partly to the fact that a larger number of "generations" are mixed in the 18° mature population.

However there is another factor which enters into these *Daphnia* fluctuations. At the higher temperature the young produced under crowded conditions are permanently less fertile than those from uncrowded cultures[10]. This phenomenon

[10]This was demonstrated by segregating newly mature specimens from crowded cultures, keeping them in isolation, and comparing their production with that of specimens reared singly, but the data cannot be applied quantitatively to these examples. Pratt did not perform the complementary experiment of crowding mature specimens which had been reared singly. However, the very sharp restriction of reproduction which occurs in such event is sufficiently indicated by the small number of progeny produced by the first young born in a culture. These live their adult (but not their juvenile) days under crowded conditions (cf. Pratt's fig. 3).

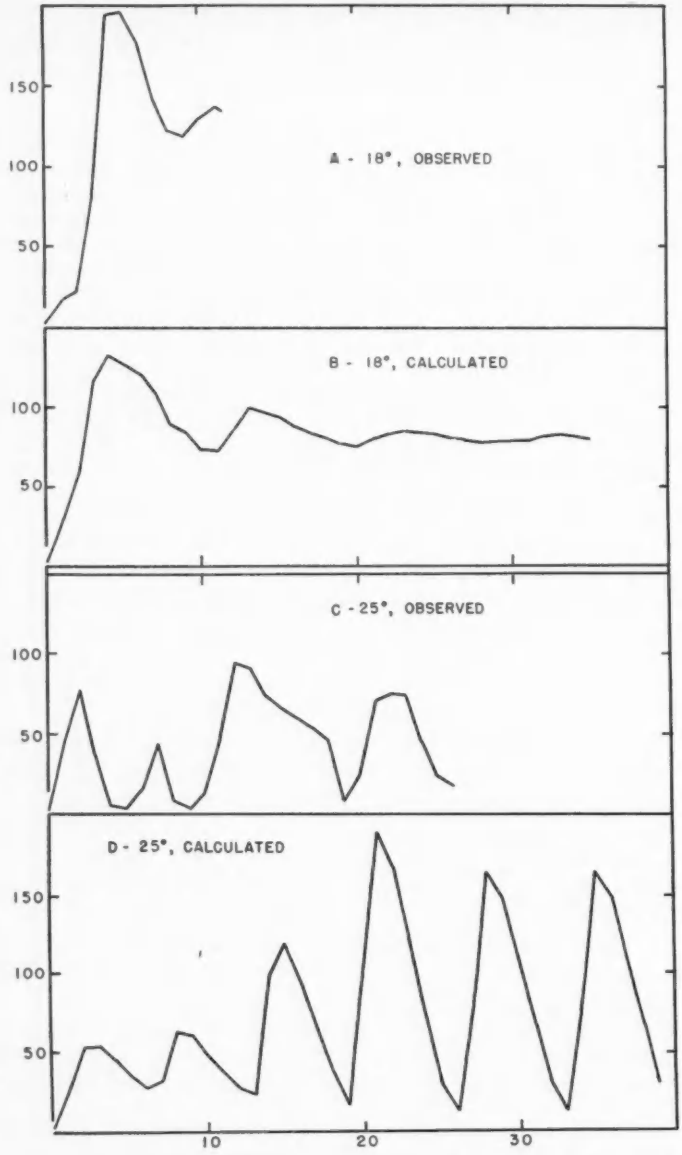


FIGURE 29. Observed and calculated fluctuations in *Daphnia* populations, from data of Pratt (1943). Curves A and C are directly from Pratt's observations, grouped by 14-day intervals at 18°C. and 6-day intervals at 25°C. Curves B and D are calculated from the reproduction curves of Figure 28. *Ordinate*—number of *Daphnia; abscissa*—successive 6-day or 14-day intervals.

has been considered the sole basis for the oscillations observed at 25°, both by Pratt and by Hutchinson and Deevey (1949). The present analysis makes it seem more likely that this effect is not an essential feature of the system, and that *actual* density is the more important depressor of reproduction.

STARFISH (*Asterias forbesi*)

No reproduction curve is available for this starfish or any other. However Burkenroad (1946) describes a series of oscillations of its abundance along the New England coast, which have had an average period of 14 years over about 90 years. These seem sufficiently remarkable to justify some speculation concerning whether they could be ascribed to a steep reproduction curve like Figure 7 or 8. If so, the implication would be that the starfish make their median contribution to reproduction 7 years after the zygote stage, and also that they make a relatively small contribution during the first few years after they are hatched. During the peaks of its cycle *A. forbesi* apparently exists in the massive numbers which would make a steep outer limb seem plausible, having in mind that starfish readily eat their own young and that reproduction is partly suppressed among individuals of crowded and poorly fed populations (cf. Vevers, 1949).

The more doubtful aspects are whether starfish live as long as a 14-year cycle would imply, and whether there is sufficient time lag before reproduction. In respect to the latter, Galtsoff and Loosanoff (1939) found the most abundant size group of *A. forbesi* at Wood's Hole in April to have a mode at only 3 cm. (between tips of arms); these would scarcely mature the same year, and even the next group, with a mode at 7 cm., could not be very fecund. The maximum size for this species is about 20 cm., which suggests a life span of several years at least, since rate of linear growth presumably falls off rapidly at the larger sizes, particularly when the stock is dense. Concerning their year-to-year mortality rate little is known except that adult starfish seem to have few natural enemies, so that for the most part they should live out a normal physiological life-span, whose length would of course probably vary a great deal from individual to individual. While they live, the number of eggs produced by each presumably increases more or less in proportion to body volume, so the number produced by a given year-class probably reaches a maximum only after it has been in existence for several years.

On the whole it seems possible, if perhaps not too probable, that the median contribution of a year-class to reproduction could be made 7 years after it was hatched, which is what a 14-year reproduction-curve cycle implies. Because so many ages would contribute to spawning, the curve would have to be very steep —probably even steeper than Figure 8—in order to produce oscillations of the amplitude described by Burkenroad, i.e., having a peak to trough ratio of about 20 to 1. There would likely be minor complications resulting from differences in growth rate between times of abundance and times of scarcity, since growth of starfish is known to vary sharply in response to availability of food. Systematic sampling for size and (if possible) for age, over a period of one or more cycles,

should provide the key to the situation. Galtsoff and Loosanoff's samples were taken in 1936–37 at a low point in the cycle, and contained large numbers of young, as expected. At a peak of abundance large individuals should predominate, and young of the year should be very scarce toward the end of the year, or sooner.

Sinuous Reproduction Curves

Dr. Pritchard's data on pink salmon reproduction at one site have already been summarized, as well as the adult counts made on the Karluk River. More recently, Neave's (1952, 1953) review of pink salmon reproduction in a number of localities has led him to suggest a rather complex reproduction situation. The species is peculiar in that there are a few areas where one of the two "lines" is completely absent in a series of streams. In other areas one line exists at a level much below the other, and the two lines will have maintained approximately the same relative position for decades, though not necessarily for the whole period of record. In still other areas there is no consistent difference between the lines in respect to abundance. Furthermore there have been cases where one line has dropped suddenly from a high to a low level of abundance and has remained at that level for a considerable period; in one or two instances such a reduced stock has bounced back up to its former level.

Dr. Neave feels that density-dependent mortality in this species must occur mainly during its freshwater life—from the time the adults appear in spawning streams in August-October to the time the fry leave in April or May. Further, there are factors causing both compensatory and "depensatory" mortality at this stage, the latter being mortality which kills a relatively larger fraction of the fish present when their numbers are small than when they are large. Experiments have shown that the activity of stream predators (trout, etc.) upon pink fry is depensatory —the fry apparently being so vulnerable that the predators eat all they can, then leave the rest alone.

This hypothesis accounting for two fairly discrete and fairly stable levels of population in pink salmon implies the existence of anomalous reproduction curves; two possible types are shown in Figures 30 and 31. (The part to the right of the dome does not enter into the argument.) In Figure 31, at some intermediate level of stock, depensatory mortality is at a maximum relative to compensatory mortality, producing the dip in the left limb of the reproduction curve. For example, a population which adhered closely to the curve of Figure 30 could be in equilibrium with a fishery taking 50 per cent of the adult fish at the two different levels of abundance indicated, but between those levels equilibrium rate of exploitation falls to as low as 20 per cent. Since 50 per cent is the maximum permissible limit of exploitation at the higher level of stock, any slightly greater exploitation will send the stock tumbling to the lower level. There it will stay unless exploitation is sharply restricted or temporarily discontinued—merely reducing it to 50 per cent again will not restore the higher equilibrium position.

More generally, when random variation in reproductive success is taken into account, the existence of a fishery makes it easier for a population to slip down

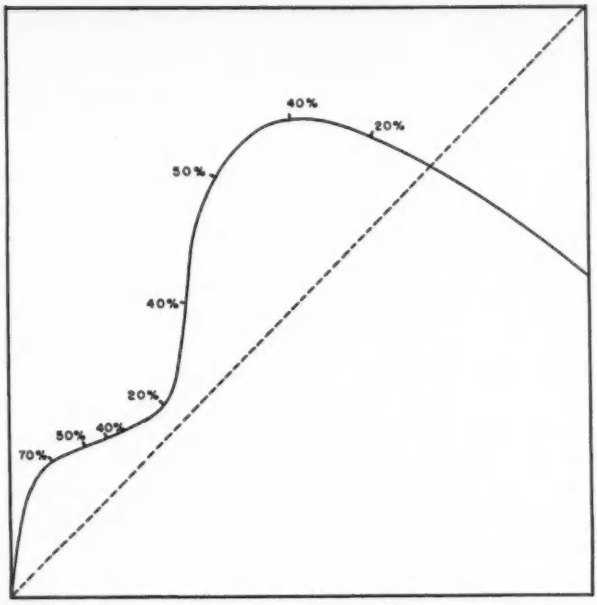


FIGURE 30. Hypothetical reproduction curve, with equilibrium positions for several rates of exploitation. See text.

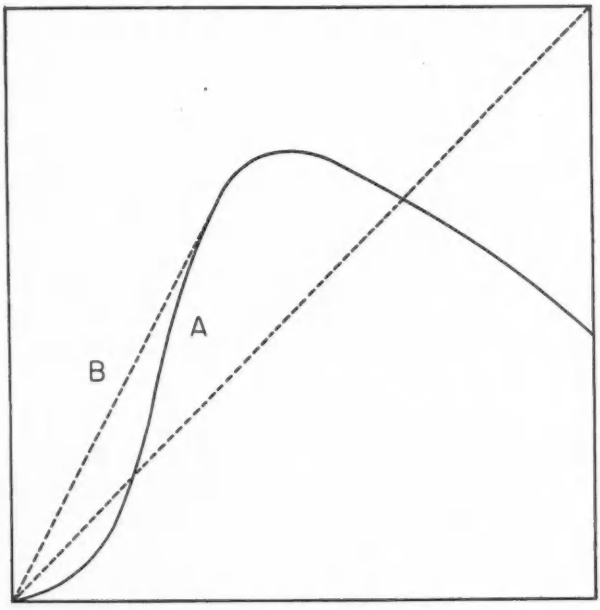


FIGURE 31. Hypothetical reproduction curves. See text.

from the higher to the lower abundance level in a bad year, and harder for it to get back up in a good one. Of course, if the reproduction curve falls off to the right of the 45-degree line, as is actually suggested in Figure 30, the *first* effect of a new fishery would be to increase population abundance.

Figure 31A differs from 30 in that there is no lower level of strong resilience to exploitation. It might represent pink salmon reproduction in areas where one of the two lines ("cycles") does not exist at all. Accidental reduction of the population past a certain low level in that case initiates a progressive decrease and results in eventual extinction. A similar situation is implied in a hypothetical net-change curve of Haldane (1953, fig. 3), and for several animals there is some experimental evidence of reduced effectiveness of reproduction at very low densities (cf. Allee, 1931; Hutchinson and Deevey, 1949).

Dr. Neave's ingenious hypotheses, illustrated by the above curves, are supported by several lines of evidence, but have not as yet been firmly established for any pink salmon stock. McClinton Creek, described earlier, is a stream which has no pinks at all in odd-numbered years, hence might be expected to have a reproduction curve like Figure 31A. The actual curve, however, is of a simple type as far as it is known (Fig. 19). If the left-hand portion of this curve falls below the 45-degree line, it must do so at densities considerably less than 5,000 female spawners—that is, in the extreme lower left corner of Figure 19B. At Karluk there is some indication of an inflexion of the curve at low stock densities (Fig. 20, upper right), but it is not clear that it is sufficient to play the role described above.

A difficulty with the curves of Figures 30 and 31A is that their initial phases are quite different, and hence it seems improbable that both should be applicable to the same species in the same general region. They might be reconciled if the beginning phase of 31A, in varying degrees of development, were commonly found tacked onto the initial part of the Figure 30 curve, producing a doubly sinuous ascending limb for the curve as a whole. If so, hypotheses as to the nature of the compensatory and depensatory mortality would have to be correspondingly more complex. A simpler but less satisfactory compromise type would have merely a straight left limb, as in Figure 31B; this would account for any observed lack of resilience in a population after a certain level of exploitation had been reached, since one density would be as stable as another once the equilibrium point had been shifted to the ascending limb of the curve.

Discussion

Doubtless other investigators will be able to add to the stock of reproduction curves from data now available, and we may expect more in the future. Considering the curves for fishes, cited above, it is unfortunate that in most cases only a section of the curve is available.

A steep ascending limb, as in Figure 2b or 8, is implied whenever a fishery consistently takes some large fraction of a stock before it has a chance to reproduce, as notably among various salmon stocks. Actual points on this ascending

limb are available in a few instances where a population has risen from or declined to a very low ebb; the Shuswap sockeye are the best example.

No curve yet discovered suggests that the maximum of recruitment is at or to the right of the 45-degree line (as in Figs. 1, 3, 4), but on several of the curves this line cannot be located.

Concerning the right limb, an indefinite horizontal extension like that of Figure 2 has often been suggested for sea fishes on *a priori* grounds (e.g., Baranov, 1918; Kesteven, 1947). Tester (1948) found this hypothesis consistent with the Vancouver Island west coast herring data, and this is still true (Fig. 18). The same can be said of some of the other curves examined (Figs. 19B, 20, 22). However, without any exception, the lines which best fit these outer limbs slant downward at least slightly, and the weight of their combined evidence

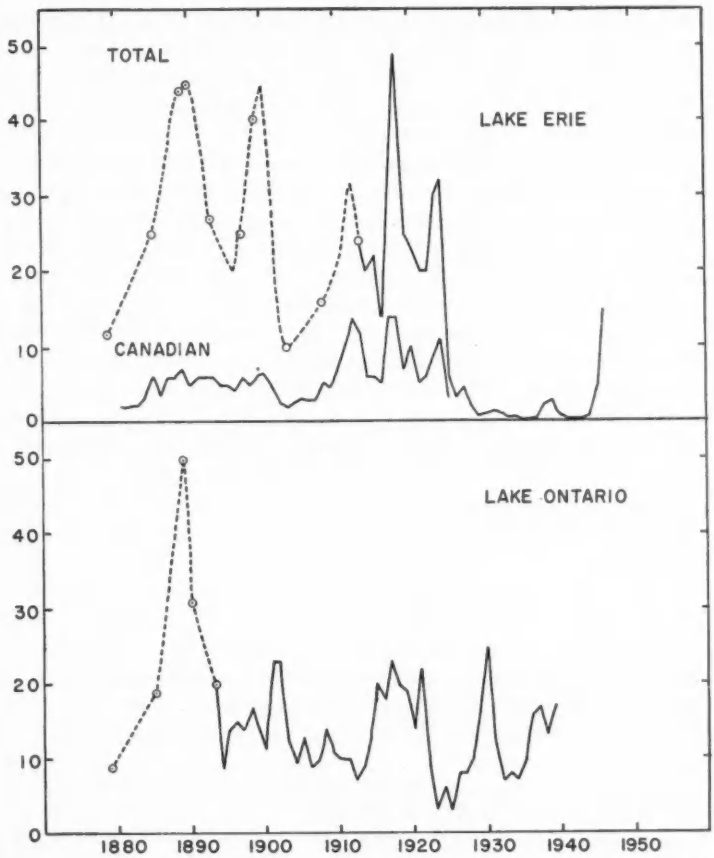


FIGURE 32. Cisco catch from Lakes Erie and Ontario, in millions of pounds. (From Gallagher *et al.*, 1943; and Scott, 1951.)

indicates that negative slopes of at least moderate magnitude are real and are the common situation. On the other hand, an approximation to the flat curve of Figure 2 might well be expected in a species like the coho, which is aggressively territorial and whose stream habitat is limited.

The best-documented example of a really steep descending limb in a natural fish population is provided by the 1912–29 New England haddock (Fig. 24), where the curve is approximately like Figure 7. Even steeper curves characterize the invertebrate populations (Figs. 26–28).

Left to themselves, steep reproduction curves produce such beautifully regular oscillations in population abundance that it is rather disappointing to discover how easily this regularity is disturbed by non-compensatory mortality (Fig. 11B). This means that we should rarely expect to be able to identify the contribution of a reproduction curve to any given series of observations of animal abundance, even though such contribution may be a major factor in many examples of marked fluctuation. And it is a fact that most of the well-known examples of fluctuating abundance cannot be a *simple* resultant of a steep reproduction curve. The 9- or 10-year cycle of grouse and hares, for example, could not be of the simple type shown in Figure 10 because there is not the necessary lag in reproduction—the young are mature in the next reproductive period after they are born; in any event it is doubtful if average longevity in these species is sufficient to put a brood's mean time of contribution to reproduction at 4.5 or 5 years. Certain major changes in fish populations—for example, cod off Greenland, herring off Norway, or mackerel off eastern North America—have occurred on too great a scale and with too long a period to have been governed by any single reproduction curve. Fish population changes having shorter period, like those of the ciscoes of Lake Ontario (Fig. 32), might be strongly influenced by their reproduction curve, but the peaks and troughs are too irregular, and basic population information is insufficient, to permit even a good guess. If the cisco rate of exploitation is moderately great, as seems probable, then direct reproduction-curve periodicity is not likely to be recognizable (cf. Fig. 17).

We are perhaps lucky to have, in Herrington's haddock, even one example of an oscillation in which the effect of the reproduction curve can be identified with fair likelihood.

OTHER REPRODUCTION SITUATIONS

Up to this point all examples and interpretations have been predicated on the postulates that it is only animals of mature size whose abundance affects compensatory mortality; and that where there is human exploitation of the stock, it takes only mature individuals. What is the effect of relaxing each of these restrictions?

Larger Immature Fish Taken by the Fishery

If a fishery takes fish of smaller than mature sizes, it makes little difference to the theory of population control outlined above *as long as the sizes subject to compensatory mortality are not touched.* Details of the equilibrium level of

population at different intensities of exploitation are of course affected, but not the general course of events. In actuality it has fairly often been found that spawning populations can be reduced to a very low level while the catch is maintained at a fairly high level by immature fish, as for example the cod in the North Sea. In this and similar instances data for plotting a reproduction curve do not seem to be available, but the general situation strongly suggests that the right limb of the curve must slope downward and that the left limb must be very steep. Until reproduction curves are available and future recruitment can be predicted, proposals for increasing catch by reducing the fishing intensity in the North Sea and elsewhere will lack that final symmetry which would make them wholly convincing.

Exploitation during the Compensatory Phase

Exploitation that takes fish at an age when natural mortality is still compensatory means, for practical purposes, a fishery for young during the first year or two of their life—the earlier the better. The removal of such young is at least partly balanced by increased survival and/or growth of the remainder; in fact, the effects of removals at this stage are equivalent to reduction of the spawning stock which produced the brood in question. If the reproduction curve for the population is of any of the types 3–8, such reduction will at first *increase* net production of recruits, which will produce more eggs and permit a larger catch of young in future years. This ascending spiral of abundance may continue until the level of stock is reached which produces maximum recruits.

There can of course be no general rule indicating a single optimum time for exploitation for all fisheries. In any particular instance, maximum yield may be obtained by taking young, or adults, or both; and in balancing the alternatives, consideration should be given to the relative value per pound of the two sizes and the ease with which they are caught. But it is clear that any *general* prejudice against exploiting young fish is unsound. Each case should be considered on its merits. The situation most favourable for juvenile exploitation is evidently that where the fish reach a *relatively* large size before compensatory mortality ceases to be important, so that the catch taken during this period can be large in total bulk.

Relatively few fisheries now exist in the temperate parts of the world which attack really young individuals, but this can be ascribed mainly to the (usually) lesser value per pound of small fish as compared with large ones, and the (usually) greater difficulty of catching these young. In Japan a number of species are eaten as larvae—for example the sand lance (*Ammodytes*). There and elsewhere the exploitation of various clupeids in post-larval, but still early, life is fairly common.

One such fishery on this continent is that for "Quoddy" herring in southern New Brunswick (Huntsman, 1952, 1953). A large primitive stock of mature herring in this region apparently fluctuated in abundance during the middle years of the last century, but no details of period or amplitude are available. About 1880 mature herring declined rather abruptly and they have not reappeared in

comparable numbers since. About the same time the weir fishery for "sardines" (age 0 to age II herring, mainly) developed enormously and has yielded large and fairly steady catches ever since—catches which bulk two or three times as great as did the early fishery for mature individuals.

If we postulate that the weirs take the young partly during the time that compensatory mortality is operative, and partly after compensation is no longer important, a formal explanation of this situation can be made. The sardines taken young, while the mechanism of compensation is still in operation, represent a diversion to human use of stock which would otherwise be lost to predators or other natural causes. The sardines taken at larger sizes, after compensation is largely finished, plus any larger stock taken, reduce the potential breeding population to a point far below the numbers it would otherwise attain (and did actually attain in years gone by). This reduced spawning stock produces many more young fish than a large one would, the implication being that in decreasing in abundance it has climbed the right limb of a dome-shaped reproduction curve such as Figure 8. In this way the present distribution of sizes and numbers could be maintained.

Compensation by Immature Members of the Population

In the restricted habitat of ponds and small lakes cannibalism is one of the most likely methods of population regulation for abundant predacious species, e.g., bass (*Micropterus*) or crappies (*Pomoxis*). Indeed, the first stages of all centrarchids are so tiny that even a normally insect-eating species like the bluegill (*Lepomis macrochirus*) may eat eggs or fry of its own species during their very early life. Immature individuals tend to be most active in this, since they normally frequent the shallow water where most spawning occurs, and gather around nests of their own or other species. Adults are less frequently in contact with young, and the males actually guard eggs and young as long as they are in the nest, or even longer; hence adults are less effective in reducing the oncoming generation. As an example, two similar ponds at the Tri-lakes Hatchery, Indiana, were stocked in spring with similar weights (13–15 kg.) of bluegills: in Pond 2 they consisted almost wholly of mature fish, in Pond 4 about half (by weight) were small fish of the previous year's brood. By November the young of the year produced by Pond 2 numbered 19,150 and weighed 36.5 kg., whereas Pond 4 produced only 230 fingerlings weighing 0.18 kg.

To adequately illustrate situations of this sort it would be necessary to construct a reproduction diagram showing the three-way relationship between quantity of mature stock, quantity of immature stock, and resulting recruitment. Present information does not permit this, but the general effect of participation of immatures in compensation must be to spread the reproduction-depressing influence of any successful brood over a longer period of time, and to make it almost impossible to have the "lag" effect which produces population oscillation. In such a situation, however, cycles of fish *size*, and to some extent of poundage, might occur if individuals of a successful brood nearly all died off during the same calendar year (cf. Thompson, 1941, p. 209).

TOWARD A THEORY OF RECRUITMENT

The justification for using any reproduction curve must in the long run come from observation. However it would be most useful, if it were possible, to formulate some general theory of reproduction which might lead to a standard type of reproduction curve applicable in a majority of situations.

Theory of Predation

An approach to this goal can be made by way of a consideration of predation upon the young of a species, whether by other animals or by older individuals of its own species. The theory of predation was briefly considered by the writer in a recent paper (1952), and the following quotation will provide a basis for the further argument here:

> It is convenient to distinguish three types of numerical relationship between predators and a species of prey which they attack.
>
> A. Predators of any given abundance take a fixed number of the prey species during the time they are in contact, enough to satiate them. The surplus prey escapes.
>
> B. Predators at any given abundance take a fixed fraction of prey species present, as though there were captures at random encounters.
>
> C. Predators take all the individuals of the prey species that are present, in excess of a certain minimum number. This minimum may be determined in different ways: (1) There may be only a limited number of secure habitable places in the environment, so that some prey are forced to live in exposed situations where capture is inevitable. The number of such secure niches may be partly governed by territorial behaviour of the prey. (2) The maximum "safe" density of prey may be the one at which predators no longer find it sufficiently rewarding to forage for them, and move to other feeding grounds.
>
> The three situations above tend to intergrade, of course, but it is useful to keep their differences in mind.

SITUATION A

This is likely to occur when a prey species is temporarily massed in unusual numbers, for example, adult herring in spawning schools, or newly-emerged fry of pink and chum salmon going downstream. The main characteristic of such situations is that the number of prey eaten depends on the abundance of predators, but not on the abundance of prey. Hence such situations cannot last long, and the predators cannot make the prey in question their principal yearly food; otherwise they would almost surely increase in abundance and the situation would change to type B or type C. If a type A situation persisted for long, it would come to an abrupt end with the extermination of the prey.

SITUATION B

Here the number of the prey species eaten is proportional to the abundance of predators and to the abundance of prey. Unlike A, this type of predation can easily occur over long portions of the year; and the prey species may comprise the larger portion of the predators' annual ration. This situation was observed at Cultus Lake, British Columbia, for predation of squawfish, char, coho and trout upon fingerling sockeye, over a wide range of abundance of the latter (Foerster and Ricker, 1941).

SITUATION C

The classical example of this situation was described by Errington for bob-white in Iowa, where a given range would winter safely a fixed number of birds, practically independently of the number which were present in autumn, the surplus being taken by predators. Studies conducted from the Atlantic Biological Station of the Fisheries Research Board of Canada,

St. Andrews, N.B., suggest that in some rivers predation upon Atlantic salmon parr tends toward type C, because a marked increase in the number of young fish planted was followed by only a relatively small increase in number of surviving smolts (Elson, 1950). In type C situtions the predators must tend to have ample alternative foods, and they are often mobile so that they can leave an area where the food supply has been "cleaned up" for the season.

Consider a prey species which is subject to type B predation over some part of its life history. Assume first that predation causes the whole of the mortality that the prey is subject to during that period. Then the prey species decreases in abundance according to the well-known exponential formula

$$N/N_0 = e^{-it}, \tag{1}$$

where: N_0 is initial abundance, N is abundance at time t, $e = 2.718 \ldots$, and i is a statistic representing the fraction of the prey which would be eaten in a unit of time if its abundance were held constant for that long; i is often called the *instantaneous* mortality rate.

Under the conditions postulated, instantaneous mortality rate is directly proportional to the abundance of predators. This can be illustrated by considering a situation where predators attack a prey population of 1,000,000 individuals under type B conditions, and they inflict losses corresponding to $i = 0.8$, where the unit of time, t, is the whole season that predator and prey are in contact. Equation (1) indicates that in, for example, 1/1000 of the season, the predators will eat $i/1000 = 0.0008$ of the prey present, or 800 fish. During the next thousandth of the season, the predators eat $i/1000$ of the surviving prey, or $999{,}200 \times i/1000 = 799$ fish. The following interval they eat $998{,}401 \times i/1000 = 799$; then $997{,}602 \times i/1000 = 798$. This continues until all the thousand time-intervals have elapsed, at the end of which there are:

$$1{,}000{,}000(1 - 0.0008)^{1000} = 472{,}400$$

survivors, or 47.2 per cent. What happens if the number of predators, is doubled? In that event, during the first thousandth of the season twice as many fish will be eaten, i.e., 1,600, leaving 998,400. In the next thousandth the fraction eaten is likewise double, namely 0.0016; multiplied by the number of survivors this gives 1,597; and so on. At the end of the season $1{,}000{,}000(1 - 0.0016)^{1000}$ survive, which is 201,900, or 20.2 per cent.

Thus doubling the number of predators doubles the instantaneous mortality rate (which is true generally), but it increases actual mortality by only $27.0/52.8 = 51$ per cent (which is true of only this particular example).

The general relation between predator abundance and actual mortality, or survival, is most conveniently expressed as:

$$\frac{p_2}{p_1} = \frac{\log s_2}{\log s_1}, \tag{2}$$

where p_2 and p_1 represent two levels of predator abundance, and s_2 and s_1 are the corresponding survival rates for the prey. This expression can easily be derived from (1), since p is proportional to i, and $s = N/N_0$ when $t = 1$.

Cannibalism

Of all the methods of population regulation listed earlier, cannibalism is the one in which the abundance of the control agent is most closely and inseparably allied to that of the population controlled. That is, an increase in mature stock not only increases the number of eggs laid or young born in a given reproductive season, but it also decreases the rate of survival of those young. What is the combined effect of these two opposed influences?

Let the size of a stock be measured by the number of eggs it lays, and let this size be proportional to its *instantaneous* efficiency in cannibalism (the fraction of young eaten by the adults in a short interval of time). Consider two situations characterized by different sizes of stock and let the ratio of the second to the

first be w, corresponding to the p_2/p_1 of equation (2) of the quotation above. Finally, let all other sources of mortality, whether they occur before, after or during the period of the cannibalism, be density-independent, their total effect being to reduce survival rate of eggs and young to the fraction k of what it would otherwise be. The number of eggs laid, in situation 1, is E_1; in situation 2 it is therefore $E_2 = wE_1$. The reproduction (absolute number of recruits produced) in situation 1 is:

$$R_1 = E_1 ks_1; \tag{3}$$

and in situation 2 it is:

$$R_2 = E_2 ks_2 = wE_1 ks_2. \tag{4}$$

From equation (2) of the quotation above,

$$w = \frac{\log s_2}{\log s_1}; \quad \text{hence } s_2 = s_1{}^w. \tag{5}$$

From (4) and (5), the reproduction in situation (2) becomes:

$$R_2 = wE_1 ks_1{}^w. \tag{6}$$

Expressed as a fraction of the reproduction in situation 1, this is:

$$ws_1{}^{w-1}. \tag{7}$$

Plotting numerical values of (7) against w, for various values of s_1, yields a family of curves each of which has an origin at zero, a dome, and an extended right limb which approaches the abscissa asymptotically. No matter what survival rate is chosen for s_1, each curve describes the whole range of possible survival values as w is varied; hence only one curve of the family is needed. The convenient one to choose is that for which (7) is a maximum when $w = 1$. To locate this maximum, (7) is differentiated with respect to w and equated to zero:

$$ws_1{}^{w-1} \log_e s_1 + s_1{}^{w-1} = 0; \tag{8}$$

whence,

$$-\log_e s_1 = 1/w; \quad \text{or, } s_1 = e^{-1/w} \tag{9}$$

The value of s which makes (7) a maximum is $e^{-1/w}$, and if this is taken as the initial value of s (that for which $w = 1$), s becomes equal to $1/e$ or 0.3679. Substituting $1/e$ for s_1 in (7), we thus finally obtain the expression

$$we^{1-w}. \tag{10}$$

This shows the actual level of reproduction as a fraction of the maximum, when w represents the ratio of the actual density of mature stock to the density which gives maximum reproduction. Values of (10) are plotted as curve B of Figure 33.

From the equations and the curve the following conclusions are evident:

1. Since the curve approximates to the abscissa as w is increased, then *if the breeding stock is made sufficiently large, cannibalism reduces reproduction practically to zero*, in spite of the greatly augmented egg deposition. In theory this is true no matter how small the original rate of cannibalism; in practice, a type B predation situation between adults and young could not be maintained over *too* wide a range of stock densities.

2. Since, as w approaches 0, e^{1-w} approaches e, it follows that at minimal densities the survival rate from cannibalism is e times the survival characteristic

of maximum reproduction. In other words, the instantaneous mortality rate at maximum reproduction is greater by unity than it is at vanishingly small stock densities (since $-\log_e (1/e) = 1$; cf. expression (1) of the quotation above).

Curve B of Figure 33 can be changed into a reproduction curve by changing the scale of each axis to represent actual numbers of parents and progeny measured in comparable units—for example the egg production unit described in an earlier section. Equation (10) gives no information concerning the steepness of this actual reproduction curve, which will depend chiefly on the magnitude of k, the survival rate from factors other than cannibalism. On Figure 33 a number of possible curves have been drawn, all based on equation (10) but using different ratios of abscissal to ordinate scales. Referring each to the 45-degree line indicated, shapes reminiscent of several of the arbitrarily drawn types of Figures 3–8 can be identified, as well as most of the curves observed in actual populations. Curve E, of course, could not describe a stable population because it lies well below the 45-degree line, while even D would be rather precarious.

In addition to cannibalism, the argument of this section can be extended to the analogous situation where strife between mature and young animals occurs and results in frequent killing of the latter, but without necessarily any eating of one by the other; this has been described among muskrats, for example (Errington, 1954). In so far as these contacts are of type B—with the older animals killing a fixed fraction of the young they encounter—they would have the same population status as described above.

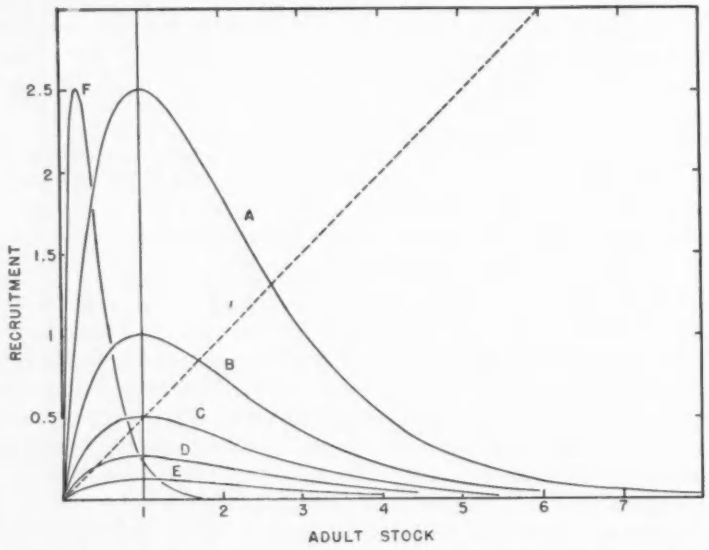


FIGURE 33. Graphs of we^{1-w} ("recruitment") plotted against w ("adult stock"). Curve B corresponds to the axes as labelled; the other curves are obtained by varying the ordinate and (for F) abscissal scales.

It is not easy to assess the probable importance, in nature, of cannibalism and allied effects. In most of the fish populations whose reproduction curves were examined earlier there is little or no evidence of cannibalism or of other direct injury to young by their parents, and among *Oncorhynchus* this is impossible because the parents die. However, in assessing the possible role of cannibalism (or any other agent of predation) in population regulation, it is not possible to weight it directly on the basis of the number of units which it kills. The latter will depend mainly upon the stage at which it is active. For example, suppose that cannibalism by mature trout fell upon their fingerling progeny following an average density-independent egg mortality of 50 per cent and fry mortality of 90 per cent (95 per cent in all); and that the adult trout ate 63 per cent of the 5 per cent remaining, or 3 per cent of the original brood. In that event cannibalism would seem to be quite insignificant either from the point of view of the percentage of the total young which it killed, or from the point of view of the frequency of occurrence of small trout in stomachs of larger trout. In spite of this, under the conditions just postulated cannibalism would be the sole mechanism regulating the abundance of the population.

Predation by Other Organisms

Even granting that lethal contact between adults and young is the most direct and least fallible population-regulating mechanism, and that it is quite apt to exist undetected, the writer's present opinion is that it will probably not prove to be important in more than a minority of populations. In its absence, other compensatory agents must take over the role of regulators which determine the shape of the reproduction curve.

TYPE B SITUATIONS. A predator can qualify as an agent of population control only if it can increase in density or effectiveness as the abundance of prey increases, and vice versa. One way this can occur is by migration of additional predator units to the region of predation when prey abundance is large. For example, greater-than-average abundance of herring spawn might attract birds from a wider area than usual. It is possible (not necessarily probable) that, after gathering together, such aggregations would remain in the vicinity for a few days longer than the supply of eggs justified it, with the result that an initially superior spawning would yield a less-than-average number of eggs hatched.

A predator might also actually increase its total abundance with that of the prey in question. Consider, for example, a plankton predator or assemblage of predators which feeds on the pelagic eggs and young of mackerel. Suppose that in years when mackerel eggs approach zero abundance these predators (which have additional foods) are numerous enough to consume the fraction $(1 - s_1)$ of the eggs. Suppose also that for each unit increase in egg numbers the average predator population increases by one-tenth of its "basic" number. (This average would be taken over the whole time that predators and mackerel are in contact because, just before the eggs are available, initial predator abundance is assumed to be the same in all years.) During the later stages of the predator-prey contact the abundance of predators would have "overshot" that of the prey, with the

result again that mackerel broods initially larger than average would end up smaller than average. From expression (2) or (7) it is easy to calculate that relative reproduction is equal to

$$Zs_1^{1+Z/10}, \tag{11}$$

where Z is the density of mackerel eggs immediately after spawning in a given year, in the unit mentioned above, and the predator density corresponding to no eggs is taken as unity. Values of (11) are calculated in Table VI, which shows the relative number of mackerel surviving the pelagic stage, for a series of initial prey densities and for two values of s_1. Sette (1943) estimated total survival of

TABLE VI. Survival rate and absolute number of survivors when average predator abundance varies with initial prey density in the manner indicated by columns 1 and 2. Pairs of survival rates and survivor numbers are shown for initial survival rates of 0.1 and 0.0001. The last two rows show the computation of the maximum number of survivors for each situation, which occurs when survival is 0.3679 ($1/e$) of its initial value.

1	2	3	4	5	6
Prey abundance	Predator abundance	Survival rate of prey	Relative number of survivors	Survival rate of prey	Relative number of survivors
			(1) × (3) × 10^3		(1) × (5) × 10^7
0	1.00	0.1000	0	0.0001000	0
0.2	1.02	0.0955	19	0.0000832	166
0.4	1.04	0.0912	37	0.0000692	277
0.6	1.06	0.0871	52	0.0000575	345
0.8	1.08	0.0832	67	0.0000479	383
1.0	1.10	0.0794	79	0.0000398	398
1.2	1.12	0.0759	91	0.0000331	397
1.4	1.14	0.0724	101	0.0000275	385
1.6	1.16	0.0692	111	0.0000229	367
1.8	1.18	0.0661	119	0.0000191	343
2.0	1.20	0.0631	126	0.0000158	317
2.5	1.25	0.0562	141	0.00001000	250
3.0	1.30	0.0501	150	0.00000631	189
4	1.4	0.0398	159	0.00000251	100
5	1.5	0.0316	158	0.000001000	50
6	1.6	0.0251	151	0.000000398	24
8	1.8	0.0158	127	0.000000063	5
10	2.0	0.0100	100	0.000000010	1
15	2.5	0.0032	47	...	...
20	3.0	0.0010	20	...	...
30	4.0	0.0001	3	...	...
1.086	1.1086	...	...	0.00003679	399
4.343	1.4343	0.03679	160	...	...

Atlantic mackerel eggs and pelagic larvae, in 1932, to lie between 0.000001 and 0.00001, so that the $s_1 = 0.0001$ column of Table VI would not be unrealistic.

The distributions of columns 4 and 6 of Table VI are of course the same as those of Figure 33. Expression (11), like (7), is a maximum when the rate of survival from the predator in question is $1/e$ of what obtains when egg abundance is close to zero (cf. Table VI). Thus we again conclude that *the instantaneous mortality rate at maximum reproduction is greater by unity than the rate characteristic of a very small population density.* For example, if $s_1 = 0.01$, the instantaneous mortality rate at minimum stock density, from the action of the controlling predator, is equal to $-\log_e 0.01 = 4.61$. At the density of maximum reproduction, mortality from this predation becomes 5.61. Mortality from other factors ($= -\log_e k$) must be added to this 5.61 to give the total average egg-to-egg instantaneous mortality rate at maximum reproduction. Note however that at the *replacement* density of stock the compensatory mortality is greater than 1, its exact value depending on the steepness of the reproduction curve (relative to the 45-degree line).

The form of expression (11) indicates that the magnitude of the arbitrary factor 10, relating initial egg density to mean predator density, does not affect the general shape of the recruitment curve, though it of course affects its steepness: the larger this factor, the broader is the range of initial egg densities which afford substantial reproduction. Furthermore the rule italicized above holds even if the relation between prey and predator is quite irregular.

Similarly, the magnitude of s_1 affects the shape of the reproduction curve only in that the smaller s_1 is, the greater is the percentage change in reproduction produced by a given change in predator abundance (Table VI).

SITUATIONS OF TYPES A AND C. So far the theory presupposes type B predation situations. Type A situations need not be discussed in detail: for reasons given earlier, they tend to be restricted in space or time, and they lack the qualifications of a population control mechanism. Their effect on reproduction curves would be to introduce irregularities such as are shown in Figures 30 and 31.

Type C situations however *can* regulate a population, and in a pure form they produce reproduction curves like Figure 2b. The horizontal part of the curve corresponds to the limit of surviving young which the habitat will sustain. Type C situations may grade into type B, in which case it would in practice be difficult to distinguish a broad-domed type B curve from the mixed type.

It is also possible for type B and C situations to follow each other, and this is examined in Figure 34. If the type B situation comes first, its typical reproduction curve is truncated by the limit of reproduction imposed later by Type C (curve A of Fig. 34). If the type C situation comes first, it will at a certain point limit the brood to a density which may be less than, equal to, or more than what gives maximum reproduction in the subsequent type B situation; these three possibilities are illustrated by curves B–D of Figure 34. Note that while the type C situation can *reduce* the difference in instantaneous mortality rate between minimal and maximal reproduction, it cannot *increase* this difference.

The various curves of Figure 34 should be looked for in nature when the biology of the animal in question points in their direction. Among the examples given earlier, a limit of environmental capacity is strongly suspected for coho salmon; actually Figure 21 could readily be fitted with a truncated curve like 34A, but there is only one point for the outer decreasing phase.

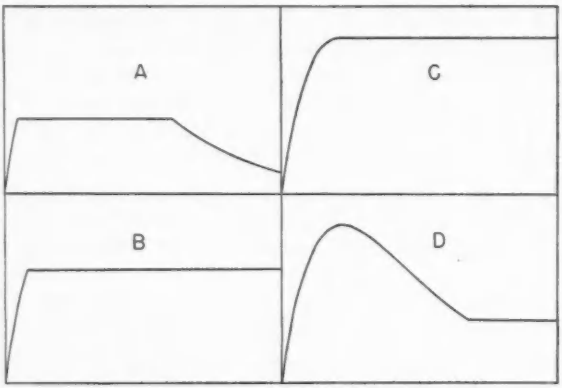


FIGURE 34. Reproduction curves when predation situations of types B and C occur in succession. *Curve* A—when type B precedes type C; *curves B–D*—when type C precedes type B. The type B reproduction curve is the same for all four situations.

SIZE OF PREDATOR AND SIZE OF PREY. It has sometimes been said that large predators (e.g., foxes) cannot control or regulate the abundance of a smaller prey species (e.g., mice), because the rate of reproduction of the prey is so much greater than that of the predator. This argument would be valid only if the predation situation were of type A, with the foxes always able to kill as many mice as interested them—a situation which could scarcely last indefinitely. However if the fox-mouse predation situation were of type B, calculations from (7) show that any increase at all in the number of foxes reduces the survival rate of mice more than proportionately, provided the foxes initially are the cause of an instantaneous mortality raté of 1 or more in the mouse broods; and the greater the increase of the foxes, the less this initial mortality need be to accomplish the result stated. To put it another way, the effectiveness of foxes in reducing the survival of mice will increase more rapidly than does the actual number of foxes, whenever they are already reducing mouse survival to 37 per cent or less of what it would be in the absence of foxes. This effect gives the foxes an advantage which tends to counterbalance the greater rate of reproduction of the mice.

More generally, there is evidently no reason why a large predator, or assemblage of predators, might not regulate the abundance of a smaller and more prolific prey species, provided their abundance can change with that of the prey to *some* extent. Indeed, since a given change in predator abundance has a greater effect upon survival, the smaller the average survival rate of the prey (and hence

the greater its fecundity), it could be argued that great fecundity should make a species more—not less—easily controlled by small changes in predator abundance. Against this must be laid the fact that great fecundity makes the prey more likely to occasionally "slip out from under" by becoming so numerous that the type B predation situation cannot be maintained.

Other Compensatory Agents

We have seen that both cannibalism and "ordinary" predation lead to the Figure 33 type of reproduction curve under type B conditions. For other compensatory agents only a qualitative examination can be attempted here, but they must be mentioned briefly.

The special type of predation situation in which insect "parasites" eat other insects regularly leads to low host reproduction at high host densities, as shown in Nicholson and Bailey's (1935) detailed analysis.

"True" parasites (those which do not regularly and consistently destroy their hosts) and disease organisms can also exhibit non-linear effectiveness which can seriously reduce reproduction at high stock densities—though their activity in this respect must usually be very irregular, if the human situation is a guide.

In the *Daphnia* cultures described earlier no predation or cannibalism existed, nor apparently did disease. The most plausible suggestion which has been made is that some metabolic product acted as a depressor of reproduction. If, for example, a metabolic waste killed a fixed fraction of *Daphnia* embryos per unit concentration and per unit time throughout prenatal life, it would have exactly the same effect upon survival as random cannibalism, and lead to the reproduction curve of Figure 33. The points of Figure 28 can be fitted by expression (10) with good apparent agreement.

Again, consider the compensatory situation where a brood, initially more numerous than average, grows more slowly than average because of competition for limited food; and because of this smaller individual size it is more vulnerable to predation than a faster growing brood at corresponding ages. It is fairly clear that here too there *could* be a lag effect whereby the brood would lose by increased predation more than the numerical advantage which it originally had; though it would be difficult to show that this should (or should not) occur as a general rule.

Finally, consider what happens when spawning facilities are limiting, as for some salmon or trout populations, for example. Natural selection will probably see to it that the population uses the best spawning facilities first. At increasing densities there is both a spread to less suitable gravel in other parts of the stream and a crowding and superimposition of eggs on the favourable grounds. With extremely heavy seeding, fungus may cover and kill almost the whole of the eggs in even the best redds; something of the sort probably decimated the Karluk pinks in the disastrous year 1924 (Barnaby, 1944). The sum of the above effects would usually add up to a domed reproduction curve with an extended right limb. Though an *exact* fit to expression (10) would not be likely, the latter might serve as a picture of the normal expectation.

FITTING THE CURVE $z = we^{1-w}$

A first approximation to a fit of expression (10) to any body of data can be obtained very quickly, because the distribution is completely determined by the position of the maximum and the latter can be selected by eye. The work consists merely of dividing each observed estimate of reproduction (Z) by the estimated maximum Z, and each observed parental stock density W by the density which produced the estimated maximum W; this gives w and z, respectively. From (10),

$$\log_e \hat{z} = \log_e w + (1 - w). \tag{12}$$

A sample calculation is shown in the last line of Table VII.

To find the *best*-fitting curve of this type it would be necessary to calculate the residuals (differences between observed and calculated values) for a series of trial positions of the maximum point. The latter can be varied in two dimensions, so the process might be fairly protracted. The accepted criterion of best fit would be that for which the sum of the squares of the residuals is least, but an easier

TABLE VII. Computation of expected reproduction ($\hat{Z}$) and residuals (R) for a set of stock-reproduction (W–Z) observations, using $z = we^{1-w}$. W = 13, $Z_{max.} = 38$, is the trial position of the dome of the curve. The last line is a computation of $\hat{Z}$ for an arbitrary W. (See text for further details.)

1 W	2 Z	3 z	4 w	5 $\log_e z$	6 $\log_e w$	7 Unity	8 R	9 R^2	10 $\log_e \hat{z}$	11 $\hat{z}$	12 $\hat{Z}$
5	18	0.47	0.38	−0.75	−0.95	1.00	−0.42	0.18	−0.33	0.72	27
8	78	2.05	0.61	+0.72	−0.49	1.00	+0.82	0.67	−0.10	0.90	34
16	20	0.53	1.23	−0.64	+0.21	1.00	−0.62	0.38	−0.02	0.98	37
28	5	0.13	2.15	−2.02	+0.77	1.00	−1.64	2.69	−0.38	0.68	26
33	8	0.21	2.54	−1.56	+0.93	1.00	−0.95	0.90	−0.61	0.54	21
78	28	0.74	6.00	−0.30	+1.79	1.00	+2.91	8.47	−3.21	0.04	1.5
Sum	..	..	..	..	..	..	+0.10	13.29	..	..	..
50	..	..	3.85	..	+1.35	1.00	..	..	−1.50	0.22	8

criterion—that the sum of the residuals should approximate to zero—would be useful in the earlier stages. Table VII shows a computation of residuals (R) for the pink salmon data of Figure 19. The dome of the curve is estimated to be at a parental abundance of W = 13 and filial abundance of $Z_{max.} = 38$. Dividing the observed values of columns 1 and 2 by these values gives z and w in columns 3 and 4. The residual (R) is the observed value $\log_e z$ less the estimated $\log_e \hat{z}$ from (12), which is equivalent to

$$R = \log_e z + w - \log_e w - 1. \tag{13}$$

The four right-hand terms of (13) are in the order of columns 4–7 of Table VII; adding columns 4 and 5 and subtracting 6 and 7 gives R in column 8, and R^2 is shown in 9. The sum of the R's is close to zero, showing that the trial position of the dome of the curve cannot be too far from the best one; however since more than half of the R^2 total is contributed by the last observation, a somewhat better fit could probably be obtained by moving the dome a little to the right or upward.

Expected reproduction values, $\hat{Z}$, are calculated in the last three columns of Table VII. Column 10 is equal to 8 less 5; or it can be obtained directly by adding columns 6 and 7 and subtracting 4 (cf. formula 12). The latter method is used to calculate $\hat{Z}$ for arbitrary values of W, as shown in the last line of the Table.

Base-10 logarithms can be used in Table VII if columns 4 and 7 are multiplied by 0.4343, but the procedure shown is more convenient when a comprehensive table of natural logarithms is at hand.

Fitted curves have not been used on the observed reproduction figures above (Figs. 18–28). Apart from the work involved, the theory of expression (10) needs further examination, and uncritical use of it now might conceal variant or alternative situations, such as that suggested for Figure 21. All the curves of Figures 18–28 were drawn freehand before expression (10) had been developed, and it is interesting that most of these observations suggested a concave and tapering right limb. Even the original hypothetical curves of Figures 7 and 8 were drawn this way, because of a feeling that reproduction couldn't really decline right to zero as spawners became increasingly numerous.

Returning to the question introduced at the start of this division of the paper, no universally applicable theory of reproduction has been discovered, or is likely to be. However several possible reasons are apparent why recruitment can decline, and usually will decline, at higher stock densities. Also, from reasonable assumptions a simple mathematical expression has been developed which could be used to represent most of the observed reproduction data over the range of densities which they cover.

SUMMARY

1. The general theory of reproduction indicates that density-dependent causes of mortality set a limit to the size which a population achieves. The "reproduction curve" for a fish species is defined as a graph of the average number of eggs produced by a filial generation against the number produced by its parental spawning assemblage, under the existing frequency distribution of environmental conditions for survival (Figs. 1–8).

2. The level of adult stock at which a *maximum number* of recruits (on the average for existing variations in environmental conditions) is obtained is not necessarily the level at which the *replacement number* is obtained (on the average). Maximum recruitment may occur either at the replacement level of adult stock (Figs. 2, 3), or at a higher level (Figs. 1, 4), or at a lower one (Figs. 5–8).

3. When, with increasing stock density, the maximum of recruits exceeds and precedes the replacement number, a population tends to oscillate in abundance. These oscillations are stable if the reproduction curve crosses the 45-degree line (representing the replacement level of reproduction) with a slope between -1 and $-\infty$ (Figs. 7, 8); they are damped if the curve crosses at any numerically lesser slope (Fig. 5).

4. Under the conditions of Figures 7 and 8 a population of single-age spawners has an irregular but permanent cycle of abundance, such as shown in Figure 11D for example, if enivronmental conditions are stable.

5. Under the same conditions a population of multiple-age spawners tends to have a more regular cycle, whose peak-to-peak period is close to twice the median length of time from oviposition by the parent generation to oviposition by all its progeny (Figs. 9F, 10).

6. For such populations to have cycles of appreciable amplitude, it is necessary that reproduction be absent or light during the first year or two of the animal's life (assuming that reproduction occurs once a year).

7. Random fluctuation in reproductive success, *by itself*, leads to very large changes in abundance and eventual extinction or fragmentation, for populations of single-age spawners (Fig. 11A), and to unlimited increase for multiple-age spawners (Fig. 12A).

8. Combinations of random fluctuation in reproduction with reproduction curves produce populations which neither increase indefinitely nor decline to extinction. The cyclical changes produced by steep reproduction curves are maintained when random fluctuation is small or moderate, but they become variable in period and eventually unrecognizable as random effects become more important.

9. Under the combined influence of a steep reproduction curve and variable non-compensatory mortality, populations fluctuate more widely than when controlled by either of these factors alone.

10. When the dome of a population's reproduction curve lies above the 45-degree line, the result of light or moderate exploitation is to *increase* the abundance of the stock in subsequent generations; more intensive exploitation will decrease it (Fig. 16).

11. Another result of exploitation is to reduce the amplitude and complexity of any reproduction-curve oscillations that may be in progress; sufficiently intensive exploitation eliminates such oscillation entirely (Fig. 17).

12. Among multiple-age spawners exploitation tends also to reduce the *period* of oscillation somewhat, because the spawning stock gradually becomes younger.

13. Reproduction curves, or approximations to them, are plotted for fish populations and four invertebrate populations in Figures 18–28. No example was discovered where the maximum of recruitment is at or to the right of the 45-degree line (as in Figs. 1, 3, 4). The left limb was usually steep. The most probable position for the right limb was always sloping downward, sometimes only slightly, sometimes quite steeply; the most typical situation has a slope about as in Figure 5.

14. Cyclic population changes that are apparently the direct result of a steep reproduction curve are those of Herrington's haddock (1912–29) and the *Daphnia* cultures of Pratt. Most other well-known cycles seem not to be of a *simple* reproduction-curve type, but the shape of this curve must profoundly influence the course of population abundance in any animal.

15. More complex reproduction curves have been suggested by indirect evidence (Figs. 30, 31), and a depression of percentage reproduction at extremely low densities of stock may be fairly common.

16. An asymmetrical dome-shaped reproduction curve can be developed from simple assumptions involving random cannibalism or compensatory preda-

tion: if w represents adult stock density as a fraction or multiple of the density which provides maximum reproduction, we^{1-w} represents the actual reproduction at density w, as a fraction of the maximum reproduction. In this event the survival rate at maximum reproduction is always $1/e$ or 37 per cent of what it is at densities near zero; or in other words, at maximum reproduction the instantaneous mortality rate from compensatory activity is 1.

17. Curves computed from the above formula, shown in Figure 33, include most of the types actually observed. However if "environmental capacity" sets an upper limit to number of survivors at some stage of the pre-adult life history, this "typical" curve could either be levelled off at any point of its course, or else truncated (Fig. 34).

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The Trophic Status of Port John Lake, British Columbia[1]

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ABSTRACT

Port John Lake is situated on King Island on the central British Columbia coast. Area is about 0.35 square miles (910,000 sq. m.). The drainage basin is 3.6 square miles (9.3 sq. km.) with an igneous foundation supporting a coniferous forest. Annual precipitation is 116 inches (295.5 cm.). An oligotrophic lake, it has a volume development of 1.53 and a mean depth of 82.2 feet (25.1 m.). The thermal stratification is second order, temperate, of the Whipple classification. The summer heat income is approximately 11,000 gram-calories per sq. cm. The ratio of O_2 in the hypolimnion to O_2 in the epilimnion is 6.58. Total dissolved solids are 39 ppm. at the lake surface.

Large amounts of organic matter are washed into the lake imposing a potential stress on its oligotrophy. However, dredge and net collections, which are dominated by chironomids and cladocerans, respectively, contained very few organisms. Plankton was most abundant in the surface water.

Low production of organisms is partly the result of the heavy rainfall which dilutes the trophic stratum above the hypolimnion, and the small amount of sunlight reaching the lake.

INTRODUCTION

In 1947 the Fisheries Research Board of Canada inaugurated a production study of Pacific salmon (genus *Oncorhynchus*) in the central coastal area of British Columbia. The investigation was centred on a small watershed at Port John where spawning escapements of pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*) and coho (*O. kisutch*) salmon were known to occur. The program was developed in part by installing fry-adult counting weirs to measure the dependence of population density on environmental conditions (Hunter,

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1948, 1949, 1951; Robertson, 1949). It soon appeared desirable to study Port John Lake because of its role as a nursery for young sockeye salmon. This is a report on the limnological results.

The program was carried on from spring to autumn in 1949 and 1950 and in the autumn of 1951. During this time physicochemical data and plankton collections were taken from two "stations" located at points thought to be representative of lake conditions. Station I was placed in the south end between the single outlet stream, Hooknose Creek, and the spawning grounds offered by Tally Creek. Station II was located farther up the lake in water close to the recorded maximum depth of 49 metres (161 feet). Surface tows for plankton were made between fixed buoys and landmarks both along shore and over deeper water. In 1949 the bottom was dredged for organisms at those points where soundings were taken. All data were taken between 1 and 6 p.m., Pacific standard time.

PHYSIOGRAPHY

Geography and Geology

Port John Lake, 52° 9′ N., 127° 48′ W., lies at an elevation of 150 feet (46 m.) on King Island, near the centre of the coastline of British Columbia (Fig. 1). King Island has an area of about 360 square miles (933 sq. km.) and contains

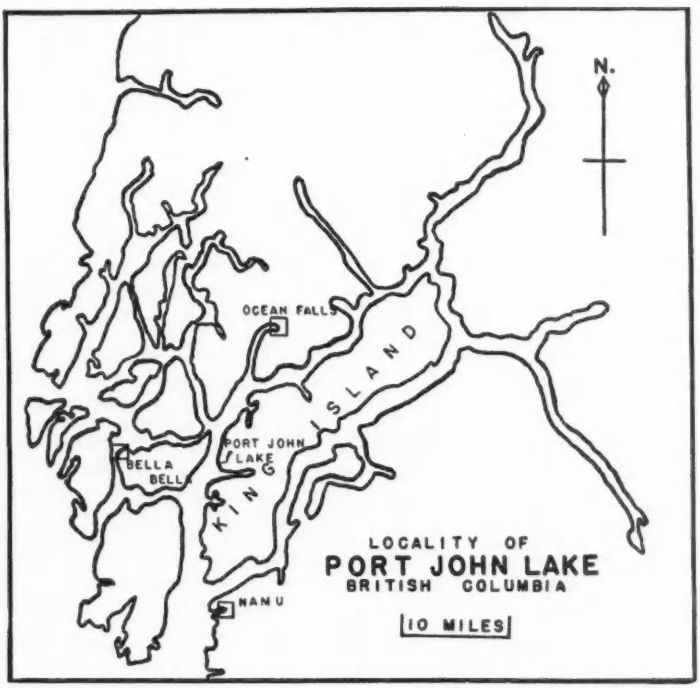

Figure 1. The central coastal area of British Columbia, showing Port John Lake and adjacent towns.

numerous lakes. Port John Lake is typical of these in that it is enclosed in a small drainage area (3.6 sq. mi. or 9.3 sq. km.). The long axis of the lake extends in a north and south direction for a distance of 1.65 miles (2.65 km.) and mountains rise abruptly to 2,000 feet (610 m.) along its east and west margins. Stands of hemlock, spruce and cedar dominate the slopes while balsam fir and alder occur sporadically.

The geological foundation is igneous and belongs to the coast range batholith. This is a belt of granite, diorite and gabbro rock 1,000 miles (1,600 km.) long and 30–100 miles (48–160 km.) wide extending from the Fraser River to the southern Yukon (Leroy, 1906; Dolmage, 1922). The batholith intruded in Upper Jurassic time and its flanks (for example, the Queen Charlotte Islands on the west) consist of volcanic and sedimentary rock of earlier origin. The batholith was left bare by vigorous erosion of Cretaceous deposits and later came under the influence of the cordilleran ice sheet.

Climate

The area under consideration may be described as a temperate rain forest (Allee and Schmidt, 1951). The precipitation at Port John, about 1½ miles (2.4

Table I. Precipitation (in inches) and average cloud cover (scale of 10) recorded at Port John Lake, B.C., in 1949–50.

1949			1950		
Week ending	Precipitation	Clouds	Week ending	Precipitation	Clouds
Apr 8	4.80	10	Apr 7	1.53	6
15	4.74	10	14	3.36	10
22	2.24	10	21	3.19	9
29	4.52	8	28	.57	7
May 6	1.87	8	May 5	1.38	9
13	.00	3	12	2.26	9
20	.24	2	19	2.23	7
27	1.80	6	26	5.76	7
Jun 3	3.90	9	Jun 2	2.15	10
10	1.94	8	9	.52	5
17	.40	4	16	.00	2
24	.67	9	23	1.59	7
			30	.52	8
Jul 1	3.98	10			
8	.02	3	Jul 7	.98	7
15	.07	5	14	1.76	10
22	1.03	10	21	.54	5
29	2.05	10	28	.41	7
Aug 5	1.11	6	Aug 4	2.52	7
12	2.51	9	11	.74	9
19	2.29	7	18	.72	6
26	.69	7	25	1.16	7
Total	40.87	154		33.89	154

km.) from the lake, in 1949 and 1950 was 111.05 and 121.79 inches (282 and 309 cm.), respectively. At Bella Bella, 12 miles (19.3 km.) west of Port John, the average annual precipitation (15 years) is 110.85 inches (282 cm.), while at Ocean Falls, 18 miles (29 km.) north of Port John, the corresponding figure (34 years) is 166.61 inches (422 cm.) (B.C. Climate, 1950).

The rainfall at Port John Lake is heavier than at other coastal sockeye lakes that have been studied limnologically. Cultus Lake, B.C. is reported to be a region of heavy precipitation with a mean annual rainfall of 62 inches (157 cm.) (Ricker, 1937b). Lakelse, B.C. (Brett, 1950) and Karluk Lake, Kodiak Island, Alaska (Juday, *et al.*, 1932) have average precipitations of 46.85 and 60.51 inches (119 and 154 cm.), respectively.

Even when rainfall was light, prolonged periods of cloud coverage were observed in the summers of 1949 and 1950 (Table I). At this time the prevailing southerly winds are generally weak but persistent in that they come up regularly in the late afternoons and last for 3 hours or so.

The annual mean air temperature at Port John in 1950 was 44°F. which is close to the 35-year average of 47°F. (8°C.) recorded at Ocean Falls. The temperature extremes in 1950 were −2°F. (−19°C.) on January 17 and 80°F. (27°C.) on June 16. The monthly mean temperatures for the year 1950 together with the average temperatures for 35 years at Ocean Falls (B.C. Climate, 1950) are shown in Table II. Such data suggest an equable air temperature, so that the ice cover present over Port John Lake from about January to mid-March in 1949 and 1950 need not be considered an annual event.

Because the lake lies between mountains it is exposed to the sun through a limited period of the day (about 8 hours in mid-summer).

TABLE II. Monthly mean air temperatures (degrees Fahrenheit) for the year 1950 at Port John, and average temperatures recorded at Ocean Falls, B.C.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Port John, 1950	13	35	37	43	48	62	58	57	54	44	35	37
Ocean Falls, 35 years	34	35	39	45	52	58	61	62	58	49	41	36

MORPHOMETRY

The morphometric features of the lake and fluctuations in the water level of the lake were studied. A polar planimeter and hydrographic chart No. 3785 (Dept. of Mines and Resources, Ottawa, Canada) were used in the study. Soundings were taken with a recording meter wheel and appropriate analytic methods selected from "Limnological Methods" (Welch, 1948).

The results of this survey are shown in Figure 2 and Table III. It is clear that Port John Lake contains a large volume of water (228.3×10^5 cu. m.) for its surface area (910,000 sq. m.). This feature is shown in the mean depth of 25.1 metres (82.2 ft.). This depth would be associated with oligotrophy by Thienemann (1927) and by Rawson (1953).

The shoreline development is moderate with a value of 2.41, and an U-shaped basin is indicated by the high volume development of 1.53. The drainage basin is small but deep. Variation in lake level is rather small: 2.55 feet or 0.78 m. in 1949 and 2.32 feet or 0.71 m. in 1950. Since precipitation is great and water

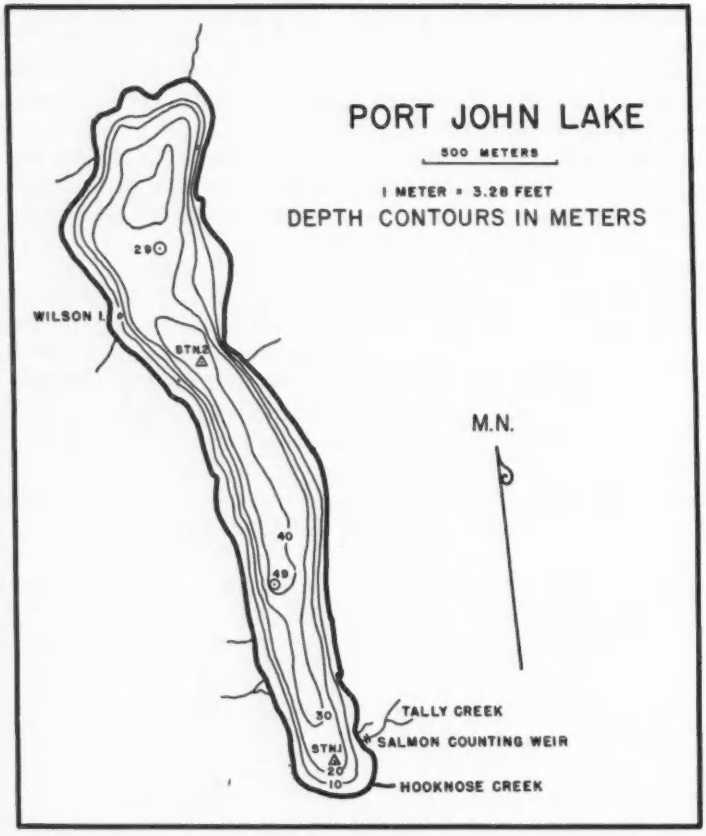

FIGURE 2. Survey map of Port John Lake.

storage is small (as shown by variations in lake level), it may be surmised that dilution and flushing of the lake suppress its productivity by removing essential plankton.

Port John Lake is almost entirely exposed to wind action from the north or south. Some shelter occurs in the southeastern corner and there a deep organic ooze and patches of sand provide a small littoral zone. The remaining shoreline usually drops abruptly into five or more metres of water.

TABLE III. Morphometry of Port John Lake (based on 77 soundings).

Mean depth	25.1 metres (82.2 feet)
Maximum depth	49.0 metres (160.7 feet)
Maximum length	2,650 metres (1.65 miles)
Maximum width	561 metres (0.35 miles)
Perimeter	6,100 metres (3.80 miles)
Area	910,000 square metres (91.0 hectares, 0.351 square miles)
Volume	228.3×10^5 cubic metres (298.6×10^5 cubic yards)
Approximate elevation	45.8 metres (150 feet)
Shore development	2.41
Volume development	1.53

Depth	Area		Percentage total area	Depth range	Volume		Percentage total volume
m.	*hectare*	*acre*		*m.*	$m.^3 \times 10^5$	$yard^3 \times 10^5$	
Surface	91.0	224.9	100	Surface to 10	81.1	106.1	35.5
10	71.5	176.7	78.5	10–20	66.5	87.0	29.1
20	61.6	152.2	67.6	20–30	51.3	67.1	22.5
30	41.5	102.5	45.5	30–40	24.7	32.3	10.8
40	11.2	27.7	12.3	40 to bottom	4.8	6.3	2.1

TEMPERATURE

Temperature determinations were made at Station I, where the depth is 21.7 metres, and Station II, depth 43.7 metres (Fig. 2). The April–May 1949 series were collected with a maximum-minimum thermometer, and July–September 1950 series with a "shallow type" bathythermograph. Where this was operated, bottom and surface water temperatures were taken with a deep-sea reversing thermometer. The latter instrument was used exclusively on all other occasions (July–December, 1949; May–June, 1950; September–November, 1951).

As in most stratified lakes there is a rise in bottom temperature at a time when the upper waters are losing their heat (Table IV). However, no temperature inversion (dicothermy) occurs. Thus, the 1949 temperatures (in degrees Centigrade) at the bottom ranged from 3.9 (April 28) to 5.5 (Oct. 18), while at the surface they varied from 5.2 (April 28) to 19.5 (July 31) and down to 9.1 (Oct. 17). In 1950, minimum and maximum readings at the bottom were 4.8 (May 31) and 5.4 (Sept. 6); the surface showed 9.8 (May 31) and 19.7 (Aug. 25). Autumn temperatures in 1951 showed a minimum reading at the bottom of 5.6 (Sept. 11) and a maximum of 6.2 (Nov. 7); corresponding surface temperatures for those dates were 17.0 and 6.8. The bottom temperature gradient may be associated with slowly advancing summer conditions, and with direct heating by the sun (Whipple, 1927).

The proximity of the thermocline (defined as a zone in which temperature changes are equal to or greater than 1°C. per metre) to the surface and a persistent stratification from May into October are characteristic of the vertical temperature distribution. Selections from these series are shown in Figure 3. There

TABLE IV. Bottom and surface water temperatures at Port John Lake, B.C., in degrees Centigrade.

Date	1949				1950				1951	
	Station I		Station II		Station I		Station II		Station I	
	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface
Apr 28	3.9	5.2	..	..	..	..	..	..	..	..
May 6	5.0	7.3	..	..	..	..	..	..	..	..
18	..	10.9	..	..	..	..	..	..	..	..
31	..	..	..	..	5.2	9.8	..	..	..	..
Jun 7	..	..	..	..	5.2	12.8	..	..	..	..
8	..	..	..	..	..	..	4.8	13.8	..	..
14	..	..	..	..	..	15.5	4.9	17.0	..	..
21	..	..	..	..	..	17.3	4.9	17.4	..	..
Jul 5	5.1	15.8	..	..	5.1	19.8	5.1	19.3	..	..
6	..	..	4.8	15.4	..	..	..	..	..	..
12	..	..	..	..	5.2	17.5	5.1	17.0	..	..
19	..	..	..	..	5.2	18.9	5.1	19.2	..	..
22	5.2	16.8	..	..	..	..	..	..	..	..
26	..	..	..	..	5.2	19.2	5.1	19.7	..	..
31	5.2	19.5	4.8	18.2	..	..	..	..	..	..

TABLE IV (*Cont'd*).

Date	1949				1950				1951	
	Section I		Section II		Section I		Section II		Section I	
	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface
Aug 3	..	..	..	..	5.2	18.5	5.1	18.1	..	..
14	5.2	15.6	..	..	..	..	..	..	..	..
15	..	..	5.0	15.0	5.2	16.7	5.0	18.2	..	..
25	..	..	..	..	5.2	18.6	5.0	19.5	..	..
Sep 6	..	..	..	..	5.3	15.3	5.4	16.0	..	..
11	..	..	..	..	..	..	..	..	6.0	15.6
19	..	..	..	..	..	..	..	..	5.6	17.0
Oct 4	..	..	..	..	..	..	..	..	6.2	14.0
17	..	..	5.3	9.1	..	..	..	..	5.7	11.3
18	5.5	9.4	..	..	..	..	..	..	..	..
24	..	..	..	..	..	..	..	..	5.7	9.3
31	..	..	..	..	..	..	..	..	6.0	8.5
Nov 7	..	..	..	..	..	..	..	..	6.2	6.8
Dec 22	..	..	4.5	4.6	..	..	..	..	..	..

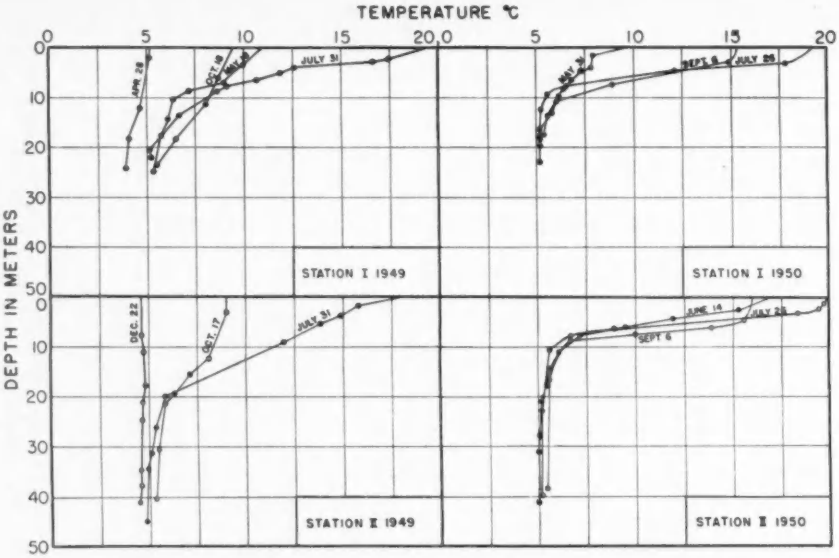

FIGURE 3. Selected temperature curves for Port John Lake in 1949, 1950.

is some fluctuation in level and thickness of the thermocline, but generally its morphometric relation is that shown in Table V. There the large volume of water (71.6%) occupied by the hypolimnion is indicated.

Spring and fall overturns were found respectively on April 28 (Station I) and December 22 (Station II), 1949. As shown in Figure 3, near-complete isothermy was present, but only in December did the temperature records approximate 4°C. In 1951 (Station I) a similar autumn thermal state was found.

The summer heat incomes (Birge, 1915) were estimated at 13,006 (1949) and 10,725 (1950) gram-calories (Table VI). The high figure in 1949 is probably the result of gap in the data at critical depths (between 10 and 20 m. on July 31, Fig. 3), rather than a change in climate. Under these circumstances the lower income of 10,725 in 1950 is regarded as more representative. This figure is apparently less than any single or average value published for Canadian lakes, but is greater than the 6,537 gram-calories given for Sodon Lake, Michigan (Newcombe and Slater, 1949). Comparative data for lakes in British Columbia

TABLE V. Typical midsummer thermal stratification of Port John Lake—Station II, July 26, 1950.

Stratum	Temp.	Depth	Volume	Volume
	°C.	*m.*	$m^3. \times 10_5$	%
Epilimnion	19.7–18.2	0–3	24.3	10.6
Thermocline	18.2–6.5	3–8	40.4	17.8
Hypolimnion	6.5–5.1	8–49	163.3	71.6

and Alaska are shown in Table VII. The disparity between Lakelse (eutrophic) and Port John (oligotrophic) under conditions of similar low heat incomes is an interesting feature, especially in view of their great differences in mean depth.

TABLE VI. The summer heat incomes (in gram-calories per sq. cm.), Station II, at Port John Lake, B.C.

1949			1950		
Date	Mean temperature	Heat income	Date	Mean temperature	Heat income
	°C.	*cal./cm.*²		°C.	*cal./cm.*²
Jul 6	7.65	9,100	Jul 5	7.68	9,200
31	9.19	13,000	26	7.79	9,500
			Aug 15	7.59	9,000
			25	8.11	10,300
			Sep 6	8.28	10,700

TABLE VII. Average summer heat incomes for some lakes of British Columbia and Alaska.

Location	Mean depth	Classification	Average summer heat income	Authority
	m.		*cal./cm.*²	
Port John Lake, B.C.	25.1	Oligotrophic	10,725	
Lakelse, B.C.	7.9	Eutrophic	11,190	Brett, 1950
Paul Lake, B.C.	34.2	Oligotrophic	15,335	Rawson, 1934
Karluk Lake, Alaska	48.6	"	18,900	Juday *et al.*, 1932
Cultus Lake, B.C.	32.1	"	23,930	Ricker, 1937

Relation of Precipitation and Lake Discharge

The influence of stream discharge into the lake on average lake temperatures will depend upon the relative temperatures of the streams and of the water displaced from the lake. In general during the summer when tributary streams may be 8°–9°C. (July 2, 1949, 8.2°, 8.3°, 8.9°C.) and the lake is highly stratified, the outflowing water will be warm (July 5, 1949, 15.8°C.) and the net effect will be to cool the lake.

With the small storage capacity of the lake, discharge under conditions of heavy rain might be expected to flush out this small but trophically important volume of water. However, this expectation is only partly met. The watershed is 93.0×10^5 square metres. Sixty per cent of the precipitation on the watershed may be expected to reach the lake (Steele, 1947). As the precipitation is relatively warm, and as the thermal stability of the lake is well established during summer, the flow of water will take place above the lower limits of the thermocline. Precipitation during the spring and summer reaches 103.8 centimetres (Table I). The volume of the precipitation reaching the lake is $1.038 \times 93.0 \times 10^5 \times 0.60$, or 57.9×10^5 cubic metres. The epilimnion and the thermocline

together have a volume of 64.7 $\times$ 10^5 cubic metres (Table V). The trophic volume is, accordingly, about 90 per cent replaced during the course of the summer. Taking annual precipitation as 295 centimetres, similar calculations show that 72 per cent of the lake's water is replaced during the course of a year. Obviously, there is a substantial flow through the lake. However, because of the relatively small watershed flushing is less marked than might be expected from the heavy rainfall.

Transparency

The limits of visibility were determined with a standard Secchi disc, as an indication of light penetration into the lake. The recommendation that the disc be used at high noon (Welch, 1935) could not be followed. Transparency recordings are presented in Table VIII. Supporting data can be observed in the amount of detritus (Table XIII, p. 642) present in the plankton collection. No measure of the dissolved organic matter was made.

The typical summer average of 4.4 metres (14.4 ft.) (Station I, II, 1950) shows greater transparency than in spring and fall. Thus the values at Station I were 3.8 metres (12.4 ft.) and 3.4 metres (11.0 ft.) on May 6, 1949, and Nov. 7, 1951, respectively. Since rainfall is greatest in the spring and fall, the decrease in transparency is the result of large amounts of organic material being discharged into the lake.

It may be noted that eutrophic Lakelse Lake has an average transparency of approximately 3 metres (Brett, 1950), a figure only slightly less than that of Port John. At Lakelse, silting, microscopic organisms and organic matter are associated with the extent of light penetration. For Port John, the light is obstructed by suspended organic matter (which imparts a brownish colour to the water). A large amount of this primary food source is a constant feature of the lake and may act as a disharmonious factor (Rawson, 1939) to the oligotrophy previously suggested. Or, as appears more applicable to the present situation,

Table VIII. Transparency recordings (Secchi disc), Port John Lake, 1949–50.

Station I, 1949			Station I, 1950			Station II, 1950		Station I, 1951		
	m.	*ft.*		*m.*	*ft.*	*m.*	*ft.*		*m.*	*ft.*
May 6	3.8	12.4	Jun 7	..	..	4.1	13.5	Sep 19	4.4	14.3
18	4.0	13.0	8	4.1	13.5	..	..	Oct 4	4.2	13.8
25	4.8	15.6	14	4.3	14.0	3.8	12.5	17	4.2	13.6
Jun 17	5.1	16.6	21	4.9	16.0	4.0	13.0	24	3.8	12.5
24	4.8	15.6	Jul 5	4.7	15.5	4.3	14.0	31	3.9	12.8
			19	4.3	14.0	4.2	13.8	Nov 7	3.4	11.0
			Aug 3	4.6	15.0	5.0	16.3			
			15	4.5	14.8	4.1	13.5			
			25	4.6	15.2	4.5	15.0			
Average	4.5	14.6		4.5	14.7	4.1	13.9		3.9	13.0

the detritus may so limit light penetration that dependent plankton production is necessarily poor (McCombie, 1953).

Mineral Content

A sample of surface water was taken in April, 1954, and arrangements were made for mineral analysis through Dr. P. A. Larkin of the B. C. Game Department (Table IX). The rather low value of total dissolved solids (39 ppm.) is to be expected from the igneous nature of the drainage area, and a calcium ion content of 4.1 ppm. indicates very soft water. Samples from below the surface are unlikely to give different assays. Rawson (1950) showed uniform mineral content in a vertical series taken in Great Slave Lake. This immense lake had total dissolved solids ranging from 22 to 160 ppm., depending on the region, adjacent rivers, and area being drained. Karluk Lake is reported to contain 30–34 ppm. total residues (Juday *et al.*, 1932).

Table IX. Partial mineral analysis of Port John Lake, from a surface sample taken April, 1954, in parts per million. Analyses made by the B.C. Research Council, Division of Chemistry.

Total dissolved solids	Sulphate ions	Chloride ions	Ca ions	K ions	Na ions
39	1.1	3.0	4.1	0.2	2.2

Dissolved Oxygen

Oxygen determinations were made using a Kemmerer water sampler and the Winkler method. All necessary precautions were observed during the procedures. The percentage saturation was calculated after determining the theoretical oxygen solubility from Figure 41 of Tully (1949).

A large amount of oxygen was found in all strata (Table X). The fact that saturation values in the hypolimnion were not less than 58 per cent indicates the oligotrophic nature of Port John Lake despite the presence of large amounts of organic matter. The oxygen demand of the organic matter in suspension and covering the lake bottom is apparently not sufficient to reduce greatly the amount of dissolved oxygen.

Other indices involving dissolved oxygen and its relation to lake productivity and organic decomposition have been developed by various authors. Of these, Thienemann's O_2H/O_2E ratio can be computed. On August 25, 1950, oxygen determinations of 8.63, 8.81, 9.59, 9.70 and 8.79 mg. oxygen per litre, were found at 43, 33, 16, 10 and 0 metres, respectively. Using the hypolimnial-epilimnial volume ratio of 71.6/10.6 at mid-summer (Table V), the O_2H/O_2E works out to 6.58, a value approaching extreme oligotrophy (Rawson, 1950).

A second index is Alsterberg's *absolute* oxygen deficit which, it may be noted, is adjustable to the *exact* oxygen deficit when the temperature and oxygen content of the water at the close of vernal partial circulation is known (Ricker, 1934, 1937b). If the present lake is assumed to have a temperature of 4°C. at vernal

TABLE X. Oxygen determinations (in percentage saturation) with corresponding temperatures (Centigrade, in brackets), Port John Lake, 1949–51. No correction has been made for the elevation of the lake (45.8 m.) in computing saturations.

	1949					1950								1951			
	July 6	24	31	Aug 14	15	Jul 26		Aug 15		Aug 25		Sep 6		Oct 4	17	24	Nov 7
Station	I	I	II	I	II	I	II	I	II	I	II	I	II	I	I	I	I
Depth *m.*																	
0	..	..	..	..	75 (15.0)	84 (19.2)	77 (19.7)	87 (16.7)	85 (18.2)	95 (18.6)	95 (19.5)	88 (15.3)	91 (16.0)	85 (14.0)	84 (11.3)	85 (9.3)	84 (6.8)
3	68 (13.0)	108 (13.0)	74 (14.8)	..	..	..	..	..	..	..	..	..	..	88 (13.6)	83 (11.3)	83 (9.3)	80 (6.8)
10	..	90 (8.2)	..	76[a] (12.9)	..	70 (5.6)	69 (5.7)	73 (5.5)	73 (6.0)	77 (6.6)	77 (6.0)	74 (6.7)	78 (6.5)	80 (8.6)	82 (11.3)	81 (9.3)	75 (6.8)
15	..	91 (5.7)	..	64 (5.6)	67[b] (5.6)	69 (5.2)	70 (5.3)	63 (5.3)	71 (5.7)	77 (5.4)	75 (5.6)	78 (5.3)	75 (5.4)	73 (7.2)	73 (6.0)	74 (6.2)	73 (6.3)
22	65 (5.2)	..	..	59 (5.3)	69[b] (5.3)	..	..	67 (5.2)	..	70 (5.2)	..	77 (5.3)	..	67 (6.2)	65 (5.7)	58 (5.7)	68 (6.2)
27	..	..	67 (5.3)	..	..	..	..	..	..	..	..	..	..	..	..	..	..
33	..	..	..	..	..	..	62 (5.1)	..	69 (5.1)	..	68 (5.1)	..	81 (5.4)	..	..	..	..
37	..	..	..	..	64 (5.1)	..	..	..	..	..	..	..	..	..	..	..	..
42	..	..	61 (4.9)	..	61 (5.0)	..	..	..	67 (5.0)	..	67 (5.0)	..	75 (5.4)	..	..	..	..

[a]7 metres.
[b]Using Aug. 14 Stn. I temperatures at those depths.

circulation, the *absolute* oxygen deficit was 3.17 by August 25, 1950. Apparently there is little oxygen depletion in this lake with so much suspended organic matter.

FLORA AND FAUNA

Bottom Fauna

In 1949 (April 28–August 24) a series of bottom dredgings were made in Port John Lake using a standard Ekman dredge collecting 520 square centimetres. The majority of the hauls contained mud, but rock and gravel were present about Wilson Island (Fig. 2) and in regions adjacent to tributary streams. All dredgings were appropriately sifted for macroscopic life using a circular screen of 20 meshes to the inch (8 per cm.). The small littoral zone was not sampled. The collections were grouped according to strata and considered on a number per square metre basis.

Table XI. Average number of bottom organisms per square metre in Port John Lake, April 28–August 24, 1949.

Depth zone (*metres*)	0–9	10–19	20–29	30–39	40 to bottom	Total
Area (*per cent*)	35.9	29.1	22.5	10.8	2.1	100
No. of dredgings	7	21	14	10	10	62
Organisms						
Oligochaeta	14	13	3	0	2	..
Chironomidae	8	23	27	4	31	..
Sphaeriidae	0	3	1	0	0	..
Total	22	39	31	4	33	..
Average	..	..	..	..	..	25.8
Weighted average	..	..	..	..	..	33.5

The number and kinds of profundal organisms are shown in Table XI. It is clear that Chironomidae (71.7%) dominate the benthic population, followed by Oligochaeta (23.9%) and Sphaeriidae (4.3%). At Cultus Lake the profundal fauna, numbering 1,087 organisms per square metre, consisted of Chironomidae and Oligochaeta in almost equal proportion, other organisms being negligible (Ricker, 1952). By comparison the entire benthic population at Port John is sparse, the average overall depths being only 34 per square metre. This value is also much lower than the 1,363 per square metre found in oligotrophic Paul Lake, a number said by Rawson (1934) to represent a moderately abundant fauna. A lower value of 799 has been found for the same lake in 1948 (Larkin *et al.*, 1950). Eutrophic Third Sister Lake in Michigan has a seasonal abundance ranging from a summer minimum of 1,500 to a winter maximum of about 70,000 per square metre (Eggleton, 1939).

The exceedingly sparse benthos described above represents spring and summer standing crops. It should be stressed, however, that in some lakes the

period of maximum abundance for deep-water bottom fauna is known to be mid-winter, a time when *Corethra* larvae are present in greatest numbers (Eggleton, 1937). *Chaoborus* (*Corethra*) larvae are present in Port John Lake, and may have been abundant over the lake floor in mid-winter.

Collections made from July to mid-August were marked by the absence of bottom organisms. Although this condition could represent a seasonal variation, it seems more likely to be associated with location; samples taken during this period were from the northern half of the lake. Thus while 50 per cent of the dredgings were from this portion, only 2 per cent of all organisms recorded were found. The oligochaetes and sphaeriids were notably absent. Their better representation in the southern end may be associated with a piling up of biogenic substances by water currents moving to the outlet (south) end of the lake.

In respect to faunal depth distribution (Table XI) the Chironomidae extended without diminution of numbers to the deepest waters, whereas the Oligochaeta appeared more abundant from 0–19 metres. Sphaeriidae were found at 10–29 metres in the region adjacent to tributary Tally Creek.

Although a large benthic population might have been anticipated from the high oxygen content of the hypolimnion and the abundant organic matter in the lake, the above findings indicate that the reverse is actually the case.

Littoral Zone

The littoral zone is of very limited area and will not be considered in detail. Its location in the southeastern corner of the lake provides reasonable shelter for rooted vegetation consisting of rushes (*Juncus* sp.) and yellow water lilies (*Nuphar* sp.). Among the plants scurry predacious whirligig beetles (Gyrinidae) and plant-feeding water boatmen (Corixidae). Water striders (Gerridae) move about the surface, while at the bottom caddis worms (Limnephilidae) are found. The area serves as a breeding ground for toads (*Bufo boreas boreas*) which are subject to predation by leeches (probably *Placobdella* sp.). Gelatinous spheres of salamander (*Amblystoma gracile*) eggs are found attached to stalks of the lilies. Various algae occur, prominent among which is the red alga, *Batrachospermum* sp. Many of the plankton species found pelagically are also present in this small but qualitatively productive zone.

Limnetic Plankton

IDENTITY OF THE PLANKTON. The following were identified from the net plankton:

Copepoda

CENTROPAGIDAE: *Diaptomus tenuicaudatus* (common); possibly *Osphranticum labronectum* (rare). CYCLOPIDAE: *Cyclops modestus* (common).

Cladocera

Pseudosida bidentata; *Holopedium gibberum*; *Bosmina longispina*; *Polyphemus pediculus*, (all common); and *Alona* (possibly *guttata*) (fairly common).

Rotatoria

Polyarthra platyptera; *Anurea cochlearis macracantha*; *Notholca longispina*; other genera including possibly *Rattulus latus* (all common).

Protozoa

MASTIGOPHORA: *Dinobryon* sp. (common).

Diptera

CULICIDAE: *Chaoborus* sp. (fairly common).

Hydracarina

Unionicola crassipes; and at least one other genus of this class (all fairly common).

Ostracoda (rare)

Nematoda (rare)

Bacillariaceae

Tabellaria sp.; *Diatoma* sp.; *Asterionella* sp. (all common); and probably other genera.

Chlorophyceae

Closterium sp. (rare); and probably other genera.

Cyanophyceae

Probably occur; *Oscillatoria* sp. was found in the littoral plankton.

FIELD METHODS. A Wisconsin-B.C. net fitted with No. 10 bolting silk was used to sample the plankton. Its efficiency was not determined. At Cultus Lake, B.C., a similar net collected Entomostraca at an efficiency close to 1.0, but nauplius larvae and very many of the phytoplankters were not adequately strained (Ricker, 1937a). Collections were made in vertical series at a time when physico-chemical data were being taken from Stations I and II, located in 21 and 43 metres of water, respectively (Fig. 2). The strata sampled were chosen according to temperature observations made at an early stage in the investigation and these depths were maintained thereafter (column headings, Table XII). All vertical hauls were made with the net closed going down and open coming up. In 1949 surface data were taken in horizontal tows over three courses: (1) east from Station I for 64 metres; (2) southeast from buoy marking (1) to the outlet bay of Port John Lake (46 metres); (3) a 160-metre surface drag down mid-lake between a landmark and buoy or landmark located equidistant from Stations I and II. In 1950 only (3) was taken. The average rates of haul, vertically and horizontally, varied between 0.32 and 0.63 metres per second.

COUNTING TECHNIQUE. A total count of the plankton samples was made by accepted methods. These involved a Sedgwick-Rafter counting cell into which were cut four rows. The plankton was concentrated in bottles to 20 millilitres (some horizontal tows were diluted two to six times, according to plankton concentration) and then shaken to insure uniform distribution. From this suspension

TABLE XII. Centrifuged volume (in *cc.* × 10^{-2}) of plankton hauls (No. 10 net), Port John Lake, 1949–50.

	Vertical series (from levels indicated to the surface)												Horizontal series		
Depth (*metres*)	44.3	43.3	37.7	30.0	25.0	21.7	19.7	16.3	13.0	9.7	6.3	3.0	0_1	0_2	0_3
Station I, 1949															
Apr 28						30	..	16	..	10	..	..	..	..	..
May 6						..	9	10	8	9	6	4	..	..	..
18						..	19	25	13	12	10	12	13	..	..
25						12	10	11	10	9	9	10	35	..	..
Jun 1						100[a]	*a*	10	10	11	5	5	18	17	..
17						19	..	12	13	13	11	8	23	22	..
24						160[a]	*a*	15	13	10	11	8	30	33	..
Jul 5						*a*	12	..	..	12	10	8	30	31	..
31						..	*a*	14	120[b]	13	11	9	24[c]	25[c]	160[c]
Aug 14						90[a]	18	11	20	..	17	..	24	26	90
27						40	..	..	..	..	..	..	..	..	650
Oct 18						38	10	9	12	10	..	..	21	..	55
Nov 13						..	..	..	..	..	..	..	..	..	21
Dec 22						9	2	..	3	2	..	2	..	..	..
Station II, 1949															
Jul 6	..	100[a]	..	..	21	..	..	17	..	9	..				
31	..	150[a]	..	..	35	..	..	22	..	19	..				
Aug 15	..	25	19	15	..	..	20	..	17	..	20				
27	..	38	..	25	16	..	15	..	15	..	16				
Oct 17	140[a]	9	..	10	9	..	..	..	10	..	5				
Nov 13	..	9	..	..	2	..	2	..	1	..	1				
Dec 22	..	..	..	2	1	..	2	..	3	..	..				

[a]Interference from bottom deposits.
[b]Interference from filamentous algae probably freed from float.
[c]Taken July 29.
[d]Taken June 7.

TABLE XII (*Cont'd*).

	Vertical series (from levels indicated to the surface)											Horizontal series		
Depth (*metres*)	44.3	43.3	37.7	30.0	25.0	21.7	19.7	16.3	13.0	9.7	6.3	3.0	0_1	0_2	0_3
Station I, 1950															
May 31						20	12	15	12	11	11	..			..
Jun 8						21	25	19	16	11	8	5			120[d]
14						10	10	10	9	10	9	12			70
21						12	11	11	11	9	10	9			90
Jul 5						14	12	13	11	9	10	9			190
19						13	12	13	10	12	9	9			650
Aug 3						22	21	19	15	19	15	16			900
15						15	11	12	11	11	..	9			580
25						24	22	22	19	18	18	15			600
Sep 6						..	13	5	8	7	7	6			300
Station II, 1950															
Jun 7	..	15	20	..	13	..	10	..	11	..	10	..			
14	..	21	22	11	23	..	18	..	13	..	19	..			
21	28	20	10	10	12	..	15	..	11	..	11	..			
Jul 5	23	20	18	15	12	..	12	..	15	..	12	..			
19	21	23	19	15	25	..	22	..	15	..	10	..			
Aug 3	..	170[a]	28	25	24	..	20	..	17	..	16	..			
15	29	..	25	19	18	..	17	..	17	..	16	..			
25	..	28	25	27	24	..	27	..	19	..	19	..			
Sep 6	27	..	10	12	11	..	12	..	11	..	9	..			

[a]Interference from bottom deposits.
[b]Interference from filamentous algae probably freed from float.
[c]Taken July 29.
[d]Taken June 7.

a suction-pipette delivered one millilitre to the counting chamber where all organisms were counted, and the amount of organic material estimated by eye as a proportion of the plankton on a 0, 25, 50, 75, 100 scale. The numerical data are presented on a cubic metre basis with the assumption that the net did not spill water.

The reliability of data derived from the fractioning technique was checked for eight common forms using Ricker's (1937a) formula (after Fisher) $\chi^2 = \frac{\Sigma(x - \bar{x}^2)}{q}$. *Polyphemus*, *Bosmina*, *Cyclops*, *Rattulus*, and *Notholca* were satisfactorily sampled, while *Anuraea*, *Holopedium*, and nauplii were not. In view of errors of collection and distribution (Ricker, 1938a) further adjustments to the micro-enumeration did not seem desirable.

TABLE XIII. Detritus in Port John Lake, 1949–50. Averages of estimates made during plankton counts on an arbitrary scale having units 0, 25, 50, 75, 100.

Date	1949		Date	1950		
	Station I	Station II		Station I	Station II	
Apr 28	30	..				
May 6	25	..				
18	35	..				
25	25	..	May 31	30	..	
Jun 1	25	..	Jun 7	..	25	
17	30	..	8	30	..	
24	25	..	14	25	30	
			21	25	30	
Jul 5	25	..				
6	..	25	Jul 5	30	25	
31	30	50	19	30	30	
Aug 14	50	..	Aug 3	25	30	
15	..	25	15	25	25	
27	25	25	25	25	25	
Oct 17	..	40	Sep 6	25	25	
18	40	..				
Nov 13	..	25				
Dec 22	25	..				
Total	390	190		270	245	1095
Average	30	31		27	27	29

VOLUMETRIC PLANKTON ANALYSIS. Following the counts, samples were returned to their bottles and centrifuged for ten minutes at 1,800 revolutions per minute.

The vertically collected volumetric data do not show a difference in means (Table XII) between stations I and II in 1949, nor between 1949 and 1950 collections. However a slight difference occurs between Stations I and II in 1950. The volumes, when compared with other oligotrophic waters, have exceedingly low values. For example, the mean centrifuged volume for Paul Lake as averaged from Larkin's (1950) data (Table II, Stn. I, July and August, 1946, No. 10 net) is 2.15 cc., whereas at Port John (Stn. I, 21.7 m., July and August, 1950) it is 0.17 cc., or 8 per cent of the Paul Lake figure.

Estimating plankton production in terms of centrifuged volume is a most unsatisfactory technique for lakes like Port John where the particulate organic material (Table XIII) leads to a false picture of abundance. To illustrate, the haul at Station I, 19.7 m., Dec. 22, 1949, contained only one or two organisms of negligible volume but the centrifuged volume of the sample was 0.02 cc. This was practically all detritus. The haul at the same Station on July 5, 1949, took many organisms and had a centrifuged volume of 0.12 cc. The amount of detritus was the same in the two samples (Table XIII), so the percentage of detritus in the July sample was only 16.7. It is obvious that plankton abundance in these centrifuged volumes is masked by the presence of detritus.

VERTICAL DISTRIBUTION OF PLANKTON. In Figure 4, an attempt has been made to associate the common plankters with the warm epilimnial water. The indicated distribution is based entirely on differences in the number of plankters per cubic metre from, for example, hauls of 21.7 and 3 metres. Averages cover three months (ten series) and no inference regarding the diurnal variation in distribution is possible.

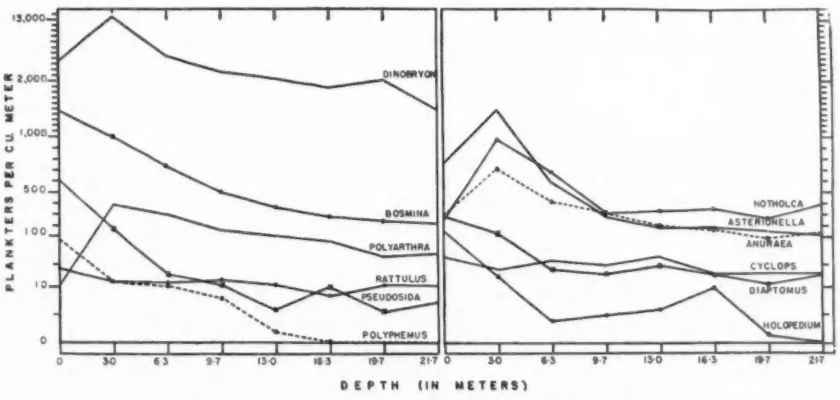

FIGURE 4. The vertical distribution of plankton in Port John Lake. Numbers represent averages taken from vertical levels considered at Station I and the 160-metre surface tows, in 1950.

The 12 species on hand are clearly most abundant in the epilimnion. The transparent diatom, *Asterionella*, was less numerous at the surface (defined as the first 25 cm. of water) than just below this level. Elsewhere (Cayuga Lake, New York), *Asterionella formosa* has been reported at all depths down to 50 metres, its abundance usually decreasing with depth (Burkholder, 1931). *Dinobryon*, a colonial protozoon, was distributed like the diatom considered. Burkholder found *Dinobryon* most abundant in the upper strata. The rotifer *Anuraea* was distributed in the same way as the two organisms named above. The other rotifers, *Notholca*, *Polyarthra* and *Rattulus*, were most numerous at the surface. The cladoceran *Bosmina* was found in considerable numbers at the surface whereas *Pseudosida*, *Polyphemus*, and *Holopedium gibberum* were most conspicuous in

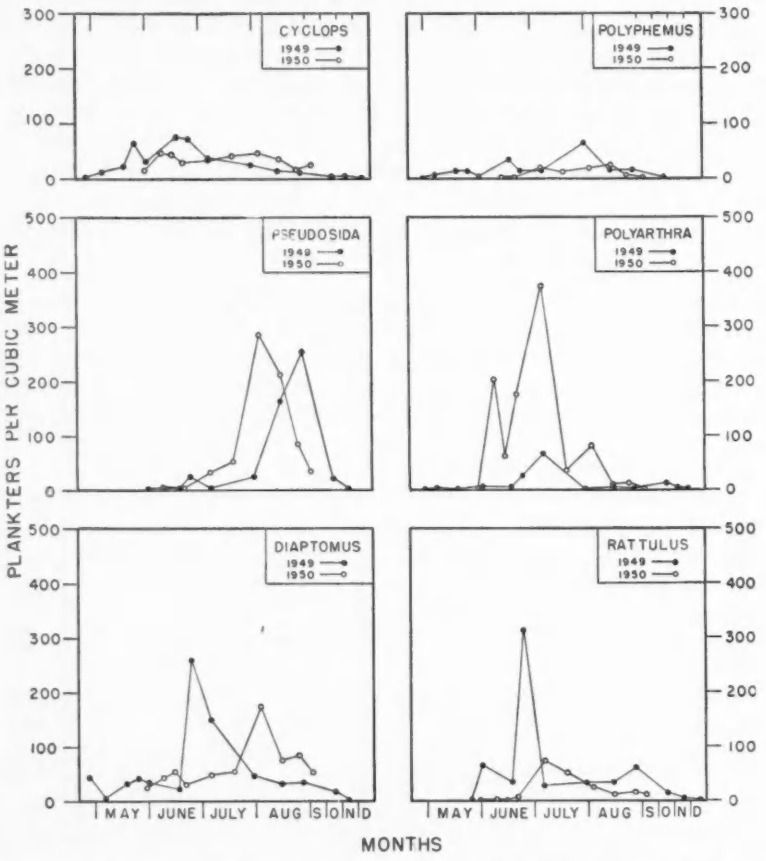

FIGURE 5. Seasonal abundance of plankton in Port John Lake, 1949 and 1950. Numbers represent averages of all data collected at Station I, II and horizontal tows. Graphic representation of Tables XIV and XV.

TABLE XIV. Average number of individual plankters taken with a No. 10 Wisconsin–B.C. net at Port John Lake in 1949. The averages are made up from the vertical series taken at Stations I and II, and from the surface limnetic hauls over three courses. The figures shown represent the number per cubic metre, on the basis of perfect filtering of the cylinder of water through which the net was drawn.

Date	*Diaptomus*	*Cyclops*	*Holopedium*	*Bosmina*	*Polyphemus*	*Pseudosida*
Apr 28	44	15	0	0	0	0
May 6	7	12	5	7	8	0
18	32	23	0	1	13	0
25	41	68	6	38	14	0
Jun 1	36	31	3	92	2	1
17	23	77	25	122	35	5
24	260	72	39	275	15	23
Jul 5	140	39	48	342	14	4
31	48	26	47	916	65	27
Aug 14	34	15	100	677	17	167
27	35	12	126	594	18	254
Oct 18	19	4	0	315	1	20
Nov 13	1	4	0	164	0	1
Dec 22	1	1	0	33	0	0

Date	*Notholca*	*Anuraea*	*Rattulus*	*Polyarthra*	*Asterionella*	*Dinobryon*
Apr 28	142	0	0	0	0	0
May 6	610	88	0	2	0	0
18	185	5	0	0	2	0
25	1610	1203	2	0	21	1
Jun 1	3114	2441	68	6	19	32
17	1634	2551	37	6	13	47
24	2616	4170	317	28	39	294
Jul 5	1093	886	30	69	25	58
31	272	194	35	0	65	15
Aug 14	99	79	36	4	50	101
27	96	116	61	1	44	145
Oct 18	28	95	15	12	15	1
Nov 13	2	13	8	2	1	0
Dec 22	1	0	0	0	3	0

sub-surface water. The last species was most often present in levels above 20 metres when taken in Lake Nipissing (Langford, 1938). In Karluk Lake, Alaska, *Bosmina* was most abundant in the 30- to 50-metre stratum (Juday *et al.*, 1932). The copepods, *Diaptomus* and *Cyclops* were also most numerous in the warm epilimnion. This observation was made on other species of the same genera by Langford (1938) and Juday (1932).

SEASONAL ABUNDANCE OF THE PLANKTON. The data which form the basis for the study of the seasonal variation in abundance of plankton are indicated in Table XII which shows the centrifuged volumes. Thus in 1949 there were 14 vertical series collected at Station I, 7 series from Station II, and 3 different

horizontal series. In 1950, corresponding data are 10 series at Station I, 9 at Station II, and one horizontal (160 metres) series. The number of a species per cubic metre of water was averaged irrespective of stratum or location for the individual dates considered in 1949, and again in 1950. The results are shown in Tables XIV and XV, and presented graphically in Figures 5 and 6. Such treatment, while tending to underemphasize the epilimnion and surface water, provides a good average of the numbers of organisms. Thus it makes use of all samples from Stations I and II as well as the horizontal tows, thereby compensating for errors arising out of the use of single stations (Welch, 1935) and variations in the horizontal distribution of plankton (Verduin, 1951). The standing crop of plankton exhibits a remarkable scarcity in comparison with other

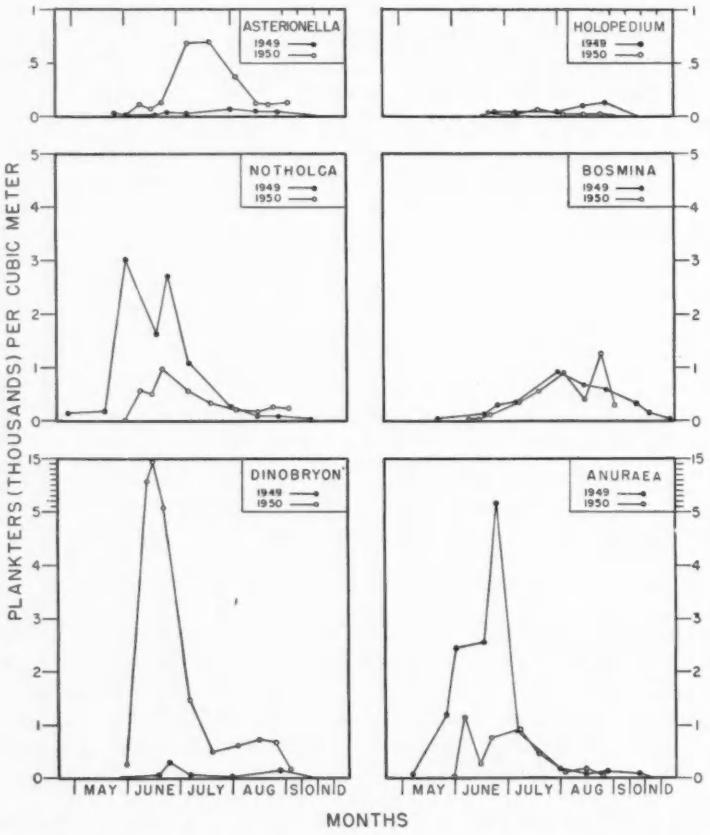

FIGURE 6. Seasonal abundance of plankton in Port John Lake, 1949 and 1950. Numbers represent averages of all data collected at Station I, II and horizontal tows. Graphic representation of Tables XIV and XV.

TABLE XV. Average numbers of individual plankters taken with a No. 10 Wisconsin–B.C. net at Port John Lake in 1950. The averages are made up from the vertical series taken at Stations I and II, and from surface hauls over 160 metres of water. Units as in Table XIV.

Date	*Diaptomus*	*Cyclops*	*Holopedium*	*Bosmina*	*Polyphemus*	*Pseudosida*
May 31	28	15	0	0	0	0
Jun 8	44	47	15	24	0	6
14	55	45	4	18	1	1
21	31	30	24	102	1	4
Jul 5	49	38	2	332	20	30
19	57	41	62	574	11	56
Aug 3	185	48	29	897	29	287
15	77	36	28	401	24	211
25	84	19	25	1284	8	87
Sep 6	55	23	7	298	0	37

Date	*Notholca*	*Anuraea*	*Rattulus*	*Polyarthra*	*Asterionella*	*Dinobryon*
May 31	9	19	0	2	11	263
Jun 8	551	1145	2	216	116	10,833
14	496	271	1	63	73	14,617
21	967	769	8	177	134	5,908
Jul 5	565	909	73	373	692	1,484
19	339	489	51	37	697	498
Aug 3	228	167	26	81	359	608
15	152	191	11	7	123	721
25	270	55	18	11	115	688
Sep 6	248	6	10	1	136	192

lakes. Such large differences cannot be attributed to collection methods, but to one or more environmental factors. These are (1) an igneous drainage basin with its sparse supply of ions many of which may be retained on land by the coniferous forest, (2) the limited sunlight resulting from excessive cloudiness, high mountain walls, and suspended organic matter (McCombie, 1953), and (3) dilution of the epilimnial habitat by the high regional rainfall.

The copepods *Diaptomus* and *Cyclops* were the only net plankton found throughout the year with the exception of the rotifer *Notholca*. Throughout summer the lake was dominated by the Cladocera and Rotifera. The protozoon *Dinobryon* differed greatly in the course of the changing abundance in the two years. Comparative detail is presented hereunder.

In the Copepoda the summer maxima of *Diaptomus* occurred on June 24, 1949, and August 3, 1950, when averages of 260 and 185 per cubic metre, respectively, were recorded. Corresponding data for *Cyclops* were 77 (June 17, 1949) and 48 (Aug. 3, 1950). Such values are far less than at Karluk Lake where minimum and maximum numbers of Copepoda per cubic metre were 1,900 (July 31, 1927) and 35,500 (Sept. 8, 1929) (Juday *et al.*, 1932). At Cultus Lake, *Cyclops* were most numerous (16,800 per cu. m.) in 1935 on May 20 (Ricker, 1938b).

Of the Cladocera, *Bosmina* had the strongest pulse, with maximum averages of 916 and 897 per cubic metre on July 31, 1949, and August 3, 1950, respectively. These pulses coincide with *Polyphemus*, but this species was less abundant (65, July 31, 1949; 24, Aug. 15, 1950). *Holopedium* and *Pseudosida* were intermediate in abundance between *Bosmina* and *Polyphemus* and appeared in maximal number at a later date. Thus on August 27, 1949, *Holopedium* averaged 126, and *Pseudosida* 254, per cubic metre. The peaks for both species were earlier in 1950, viz., 62, July 19; 287, August 3, in order. The cladoceran fauna of Karluk Lake included *Bosmina* sp. and *Daphnia* sp. and these, like the copepods, were far greater in number (maximum, 8,100 per cu. m., Sept. 3, 1928; minimum, 400, July 12, 1930) than those of Port John Lake. In Cultus Lake, there were fewer species of Cladocera but individuals were more numerous, reaching 11,340 per cubic metre by May 20, in 1935 (Ricker, 1938b).

The rotifer collection was composed of many species, not all of which were identified. The dominant species can be discussed in order of abundance. *Anuraea* was most numerous in June of both years but less abundant in 1950. Thus the maximal averages were 4,170 (June 24, 1949) and 1,145 (June 8, 1950), per cubic metre. *Notholca*, with maxima of 3,114 (June 1, 1949) and 967 (June 21, 1950), had a seasonal pulse almost coincident with that of *Anuraea*. *Polyarthra* showed a series of pulses in 1950, but had only one peak in 1949. In that year it was most numerous on July 5 (69 per cu. m.), but the average was far less than a similar peak in 1950 (373, July 5). Contrary to *Polyarthra*, *Rattulus* was more abundant in 1949 than in 1950, the maxima being, respectively, 317 (June 24) and 73 (June 5). At Karluk Lake the numbers of Rotifera ranged from 17,200 to 367,000 per cubic metre, with seasonal pulses of the dominant *Asplanchna*, *Anuraea* and *Polyarthra* occurring in July and September (Juday, *et al.*, 1932). As at Karluk, the Cultus Lake rotifers (Ricker, 1938b) were far more abundant than those of Port John Lake. Differences here may be attributed in part to the No. 10 net used at Port John Lake and the plankton traps used on Karluk and Cultus Lakes.

The protozoon, *Dinobryon*, showed a remarkably different abundance in 1949 and 1950 collections. The difference is reflected in the pulse which in 1949 was greatest on June 24 (249 per cu. m.) and in 1950 on June 14 (14,617). Again, these numbers are much less than recorded for Protozoa at Karluk, and *Dinobryon* at Cultus, and differences may be again the result of the less adequate No. 10 net used at Port John.

Fish Life

The present paper does not attempt to discuss the fish populations and their biotic interrelationships in Port John Lake. However, it is evident that feeding conditions must greatly limit production of fish.

The lake supports a comparatively small population of young sockeye salmon and a few coho salmon. A rough calculation from data of J. G. Hunter (unpublished), Brett (1950) and Foerster (1938) shows that Port John, Lakelse and Cultus Lakes have sockeye smolt productions of the order of 40, 160 and 300 per acre, respectively. A small trout population is indicated by sport fishing records

and limited gill-netting by investigators. Species taken were cutthroat (*Salmo clarki*), rainbow (*S. gairdneri*) and Dolly Varden (*Salvelinus malma*). Other resident fish are the sculpin, *Cottus asper*, and stickleback, *Gasterosteus aculeatus*. Since the sea lamprey, *Entosphenus tridentatus*, was found in tributary streams, it is likely present at one time or another in the lake.

SUMMARY AND CONCLUSION

The trophic status of Port John Lake has been dealt with progressively according to well known indices. It is clearly an unproductive lake of an extreme type. Strøm's (1928) remark that "the biological processes in a lake are largely governed by its own physical conditions" is well suited to the present case.

Port John Lake has an area of 910,000 square metres and a mean depth of 25.1 metres. It lies in a small but precipitous drainage area which supports a coniferous forest. The thermal stratification is second order temperate, and the summer heat income amounts to 11,000 gram-calories. There is no serious oxygen depletion as shown by the O_2H/O_2E value of 6.58. The low content of total dissolved solids (only 39 ppm. at the lake surface) reflects the geological environment. Light penetration is poor as a result of suspended organic matter, excessive cloudiness and high mountain walls.

While the above-mentioned conditions contribute to the oligotrophic status of the lake, there is a disharmony imposed by the large amount of organic matter washed into the lake. The stress introduced by this eutrophic factor could be released by the tendency toward flushing by the intense rainfall which amounts to 116 inches annually. However, when the precipitation was considered in relation to the watershed, it was found that 90 per cent of the lake volume above the hypolimnion was being replaced under conditions of typical summer stratification and spring and summer precipitation of 103.8 centimetres. The annual replacement of the entire lake was 70 per cent. This greatly contrasts with Upper Campbell Lake whose volume of 2.7×10^8 cubic metres is replaced in about two weeks (McMynn and Larkin, 1953). The flushing was a dominant factor in limiting production of that lake, but in the present case the precipitation acts mainly as a diluent.

Oligotrophy is observed in the almost barren benthic region where 62 dredgings returned only 19 chironomids, 6 oligochaetes and 1 sphaeriid per square metre. Similarly the pelagic plankton, dominated by the Cladocera so far as fish food organisms are concerned, is never numerous. The littoral zone is not significant in the economy of the lake. The lake supports a comparatively small population of young sockeye salmon, while coho salmon, trout, cottids and sticklebacks make up the remaining species of fish.

In this lake the trophic status is so modified by the complexity of its physical conditions that it is doubtful if the descriptive term oligotrophy has any real meaning except to indicate a relative level of production appropriate for comparison with other lakes in the Pacific Northwest. This emphasizes the importance of a regional concept of productivity of lakes and the difficulty of extrapolating schemes of lake classification over wide geographic areas.

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The Relative Growth of Hybrid Char (*Salvelinus fontinalis* × *Cristivomer namaycush*)[1]

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ABSTRACT

Hybrid char from Banff were intermediate between the two parental species, lake trout and eastern book trout, in respect to relative growth of some characters; in others they approximated one or other of the parent species. However it was not possible to make comparisons with parent-species material of the same stock as the hybrids' parents and reared under the same conditions.

INTRODUCTION

The relative growth method of analysis of body form has been of interest since the publication of the works of Crozier and Hecht (1914) and Hecht (1916) and its development by Huxley (1932). Still earlier workers in this field were Paton (1898) and Fulton (1905). In the present investigation attention has been directed toward the study of the relation between the standard length and the length of various body parts in a series of hybrid char.

MATERIAL AND METHODS

One thousand eggs of the lake trout, *Cristivomer namaycush* (Walbaum), which had been fertilized with the milt of the eastern brook trout, *Salvelinus fontinalis* (Mitchill), were received at the Laboratory for Experimental Limnology at Maple, Ontario, from Banff National Park. These hybrids were produced by Mr. J. A. Stenton. Before receipt at the laboratory at Maple the eggs had been held at 5°C. After receipt the material was held at temperatures which ranged with the season from 7.2° to 9.2°C. The young fish were fed liver daily except Sunday. Samples of about ten individuals were taken every one or two weeks beginning January 8, 1951, and continuing for more than a year, comprising in all 392 individuals. The samples were preserved in 10 per cent formalin and measured after preservation. The dates of sampling are recorded in Table I. Measurements were made with vernier calipers graduated in half-millimeters and each measurement was estimated to 0.1 mm. The size range represented in the samples was from 15.5 mm. to 84.5 mm. standard length. (The length range extended to 145 mm. for measurements of eye diameter, pectoral and ventral length.) To smooth out individual variation the measurements of from two to three samples were combined as indicated in Table I. In order to compare the fish with the parent species the same measurements were made as Martin (1949)

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used, who has published the most extensive series of data on them. The following measurements were made:

1. STANDARD LENGTH—Distance from the tip of the snout to the end of the last caudal vertebra.
2. HEAD LENGTH—From the tip of the snout to the posterior margin of the operculum (without the membrane).
3. EYE DIAMETER—The uncompressed eyeball was measured in a horizontal plane.
4–5. PECTORAL and VENTRAL LENGTHS—From the base of the fin to the tip of the longest ray.
6. ANAL HEIGHT—From the origin of the anal fin to the tip of the longest ray.
7. DORSAL TO CAUDAL—Distance from the posterior origin of the dorsal fin to the end of the last caudal vertebra.
8. SNOUT TO DORSAL—Distance from the tip of the snout to the origin of the dorsal fin.
9. DEPTH—Vertical distance through the body at its deepest point.
10. WIDTH—Horizontal extent of the body at its widest point.
11. WEIGHT—Total weight in grams after preservation.

The data were treated in the conventional method of relative growth plots (Huxley, 1932) in which the dimension of the part is plotted against the dimension of the body on a double logarithmic grid.

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The eggs for this study were presented to the laboratory through the courtesy of the Dominion Wildlife Service. The work was carried out in the Laboratory for Experimental Limnology at the Southern Research Station, of the Ontario Department of Lands and Forests, Maple, Ontario. This laboratory is operated jointly by the Ontario Department of Lands and Forests and the Ontario Fisheries Research Laboratory, Department of Zoology, University of Toronto. Financial assistance for the work was received from the University of Toronto Research Fund. The problem was suggested by the Director of the Laboratory, Dr. F. E. J. Fry. I am indebted to Dr. J. M. Speirs for literature.

RESULTS

The heavy lines and the solid points in Figures 1, 2 and 3 represent double logarithmic plots of the measurements of the body parts of the hybrids against the standard lengths. The points represent the data summarized in Table I: each point represents the individuals preserved at one time. To afford a comparison with the parent species, Martin's (1949) data for the brook trout are shown as broken lines with circles, and his data for the lake trout as broken lines with crosses. These data were chosen since they cover approximately the same size range as that covered by the hybrids, and the measurements of the parts were taken in a similar manner.

Each family of relative growth curves presented in the figure will be discussed in detail below. The discussion in each instance is centred about the typical interpretation of relative growth curves put forward by Huxley (1932)

TABLE I. Summary of measurements on 392 hybrid trout. The values given are the means for the sample, in millimetres.

Date	No. of fish measured	Standard length	Head length	Eye diameter	Pectoral length	Distance from caudal to dorsal	Depth	Width	Anal height	Dist. from tip of snout to dorsal	Ventral length	Weight (*grams*)
1951												
Jan. 8–15	20	17.18	3.31	1.46	2.03	9.22	4.91	2.02	0.79	8.16	0.83	0.10
Jan. 22–30	20	20.28	4.25	1.84	2.47	11.15	4.96	3.30	1.17	9.79	1.31	0.11
Feb. 5–13–21	30	22.64	5.29	2.03	3.56	12.24	4.68	3.00	2.31	11.20	2.20	0.13
Mar. 5–12–19	30	26.92	6.47	2.32	4.66	14.20	5.20	3.16	3.42	13.16	3.27	0.19
Apr. 3–18	20	30.13	7.55	2.66	5.21	15.99	5.55	3.39	4.11	14.87	3.99	0.29
May 4–18	20	34.01	8.68	3.04	5.90	17.79	6.75	4.14	5.17	16.86	4.76	0.49
Jun. 11–29	20	36.36	9.69	3.40	6.87	19.46	7.33	4.68	5.69	18.42	5.31	0.65
Jul. 23	10	42.23	11.55	3.65	7.72	22.75	8.56	5.57	6.32	21.23	6.06	0.98
Aug. 14	20	46.82	12.66	4.05	8.61	24.97	9.76	5.94	7.05	23.01	6.84	1.46
Aug. 16–17	20	49.95	13.24	4.16	9.23	27.05	10.64	6.88	7.49	24.16	7.22	1.67
Aug. 22–29–30	30	50.90	13.62	4.24	9.47	27.32	10.49	6.41	7.72	26.90	7.37	1.82
Sep. 5	20	53.91	14.16	4.31	9.90	29.29	11.46	7.36	8.05	26.13	7.66	2.34
Sep. 6–7	20	56.56	14.99	4.58	10.29	30.90	12.52	8.11	8.66	27.01	8.24	2.79
Sep. 11–18	18	59.55	15.74	4.69	10.79	32.96	12.17	8.44	9.04	28.24	8.85	3.20
Oct. 5–15	25	54.56	14.82	4.46	10.12	29.70	11.90	8.07	8.00	26.18	7.80	2.52
Nov. 8–27	16	66.79	17.15	5.00	12.41	35.70	12.35	8.17	10.11	31.63	9.99	3.81
Dec. 2–3	15	63.55	16.53	4.95	12.15	34.43	12.01	7.30	9.43	29.94	9.37	3.07
Dec. 5–10	19	65.29	17.12	5.18	12.29	35.12	12.61	7.91	9.63	31.22	9.50	3.65
Dec. 5–10	19	65.29	17.12	5.18	12.29	35.12	12.61	7.91	9.63	31.22	9.50	3.65
1952												
Jan. 4–15–17	19	70.49	18.18	5.35	13.63	38.27	13.46	8.42	10.34	33.14	10.38	4.22

and exemplified in the case of fish by Martin (1949). In this interpretation it is ordinarily taken that the relative growth history of a given body part can be expressed by a series of one or more straight lines on a logarithmic grid with more or less sharp inflections or discontinuities between them. The slope of the relative growth line represents the relative rate of growth of the part as compared to the body. The numerical expression of this slope as the tangent is designated the growth partition constant. When the growth partition constant is greater than unity, that is, when the part is growing at a rate relatively faster than the rate of the body as a whole, the relative growth pattern is spoken of as *tachyauxesis*. When the reverse is true and the growth rate of the part is relatively slower the pattern is that of *bradyauxesis*. If the rates of the part and the whole are equal and the slope is exactly unity, then the pattern is termed *isauxesis*. Intervals during which the relative growth pattern is constant are termed stanzas. For a recent summary of the terminology and bibliography of relative growth see Martin (1949).

Pectoral Length

The curves for this character are shown uppermost in the left hand series of Figure 1. Over the size range for which data are available for comparison,

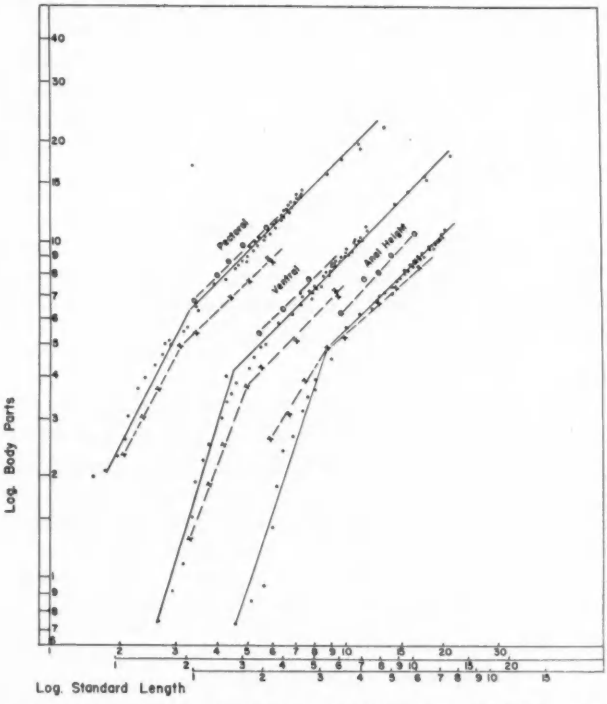

Figure 1. The relative growth of the body parts of hybrid, brook and lake trout. Open circles: brook trout; dots: hybrids; crosses: lake trout.

Martin's relative growth lines for the brook trout and lake trout are parallel, with the brook trout having the longer fins. His data for the lake trout, which extend down to a smaller size than do those for the brook trout, show an inflection at 31 mm. standard length where the growth partition constant changes from bradyauxesis to approximate isauxesis. There is indication of an inflection in the same direction in the curve for the hybrid (which up to that point lies above the lake trout line and apparently parallel to it) that occurs at approximately 33 mm. standard length, at which length the fin has approached more closely to the dimensions of that of the brook trout. At greater lengths the growth of the pectoral appears to be essentially isauxetic, and the relation appears to follow closely that for the brook trout.

Ventral Length

The same picture of relative growth is seen for the ventral fin as was found for the pectoral, a drift from a relative size similar to that of the lake trout in the first stanza investigated to approximately the relation displayed by the brook trout in the second stanza. The inflection shown for the relative growth curve for this fin comes at 28 mm.

Anal Height

During the first growth stanza covered by the measurements, the anal height in the hybrid is relatively smaller than in the lake trout and presumably also smaller than in the brook trout. However, the growth of the anal is strongly tachyauxetic at this stage, and at the point of inflection the fin is of the same relative size in the two stocks. Beyond the point of inflection the lines for the lake trout and the hybrid lie close to each other, but the hybrid may possibly have a slightly greater slope.

Dorsal to Caudal

In the data presented the brook trout has the longest relative dorsal to caudal distance, the lake trout has the shortest, and the hybrid is intermediate. The slopes of the lines for the three species are similar. There is possibly an inflection at the lower end of the hybrid curve.

Body Depth

Martin (1949), over the ranges covered by his data, interpreted the relative growth curve for this character in the brook trout as a single straight line and that of the lake trout as two straight lines. The first stanza that he recognized as being displayed in the lake trout occurred at sizes smaller than any of the brook trout he measured. The data for the hybrids fall between Martin's data for the parent species but do not clearly display an inflection such as he found for the lake trout. The smallest hybrid specimens measured show a decrease in body depth with increasing size. This is associated with the absorption of the yolk sac.

Body Width

The relative growth in body width behaves in the same manner as was found for body depth. Martin put a slight inflection at the lower end of the lake trout

line for this character also, for which no corresponding inflection was found in the hybrid.

Eye Diameter

While Martin interpreted the relative growth of the eye in the parent species as each following a single straight line on a logarithmic plot, the points for the hybrids fall on at least two lines or perhaps better still on a smooth curve which takes them now adjacent to the lake trout line and later adjacent to the brook trout line. In Figure 2 the interpretation has been given as a curve. In the larger fish the eye appears to be relatively smaller than that of the lake trout as judged by extrapolation of Martin's line.

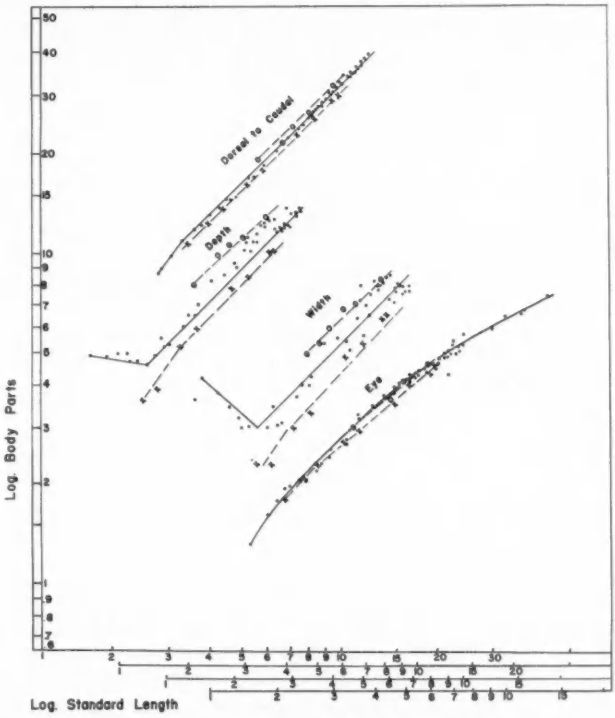

Figure 2. The relative growth of the body parts of hybrid, brook and lake trout. Open circles: brook trout; dots: hybrids; crosses: lake trout.

Head Length

This character is plotted in Figure 3. There is very little difference in the relative head lengths in the two species and their hybrid in the measurements presented and all three show the same trend. Both the lake trout and the hybrid display a definite inflection point at 30–35 mm. where the pattern changes from

tachyauxesis to approximate isauxesis. The data for the brook trout represent only the second stanza, presumably because none of the specimens were small enough to fall into the first. In comparison with Martin's data, the hybrid is not intermediate between the parents in respect to this character but lies below the brook trout.

Snout to Dorsal

This character is also plotted in Figure 3. The lines for the lake trout and the brook trout are parallel where they can be compared, with the brook trout having the shortest snout to dorsal distance. The hybrid is intermediate and appears to drift from the lake trout to the brook trout line. At the lower ends of the lake trout and the hybrid curves there appear to be inflections, but Martin does not consider this inflection in the lake trout to be of any appreciable magnitude although he presents two lines in his figure. It is, if anything, still less marked in the hybrid and has been disregarded.

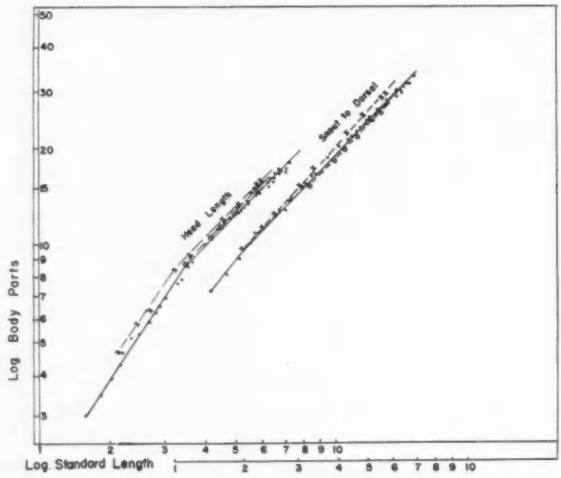

Figure 3. The relative growth of the body parts of hybrid, brook and lake trout. Open circles: brook trout; dots: hybrids; crosses: lake trout.

DISCUSSION

The hybrid tends to be intermediate between the representatives of the parent species which Martin measured, although this is not always the case. Certain characters, pectoral and ventral lengths, anal height and eye display relative growth relationships which tend to approximate one parent line or the other rather than to fall between them. In the eye diameter the hybrid line falls below the parental line at its upper extremity. Head length is never intermediate as far as can be judged.

However, because of the great intraspecific variation in body form displayed by the salmonoids, which, as Martin and Wilder have shown, is expressed in changes of intercept of the relative growth lines, a strict comparison of the positions of the hybrid and parental lines presented here has no great meaning. The curves given for the parental species are not for the actual parental stocks. Neither are they curves for members of the parental species reared under the same conditions as were the hybrids. Thus, there are possibilities of both genotypic and, what is probably more serious, phenotypic deviation of these two samples from a group that would be strictly comparable with the hybrid sample.

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Annual Growth Rings and Rate of Growth of the Giant Scallop, *Placopecten magellanicus* (Gmelin) in the Digby Area of the Bay of Fundy[1]

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ABSTRACT

The growth rings on the valves of scallops collected from the Digby area of the Bay of Fundy are formed only once a year during the winter. Observations of special collections of small scallops have also shown the position of the first growth ring. This information has been used to construct a general growth curve from measurements of annuli on scallops from the Digby area.

INTRODUCTION

Seasonal variations occur in the rate of growth of many organisms and give rise to distinctive annual marks on their growing hard structures. Such marks have been widely used to identify year-classes in studies of populations of fish and lamellibranchs, and, together with suitable criteria of size, have facilitated growth studies of a variety of animals.

In the giant scallop, *Placopecten magellanicus* (Gmelin), lines of growth appear as fine concentric striae on the outer surface of the valves. These striae have been described and figured by Verrill (1897) and Drew (1906). Their spacing follows a regular pattern. Relatively wide spacing (0.8 to 1.0 mm.) alternates with crowding and gives the appearance of bands of growing shell separated at intervals by slightly roughened or thickened rings (Fig. 1). This pattern is suggestive of a seasonal growth cycle, rapid growth in summer alternating with slow growth such as has been found to occur in winter in other lamellibranchs along the Northwest Atlantic Coast, notably *Mytilus edulis* (Mossop 1922), *Mya arenaria* (Newcombe 1935), *Venus mercenaria* (Kerswill 1941), and *Spisula solidissima* (Kerswill 1944), or at the time of spawning in *Pecten irradians* (Gutsell 1930). If the rings formed by the crowding of the striae are annual rings, they provide a convenient method for determining the age of scallops.

In previous studies dealing with the growth of shallow-water lamellibranchs it has been possible to show in certain cases that some of the growth rings on their shells are annual rings by direct observations of the growth of a number of

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[2]This paper was composed by the junior author, but is largely based on observations and experiments by J. A. Stevenson, Temporary Scientific Assistant at the Atlantic Biological Station from 1931 to 1936, and reported by him in his MS Reports to the Fisheries Research Board of Canada. Mr. Stevenson was drowned in the course of his 1936 investigations.

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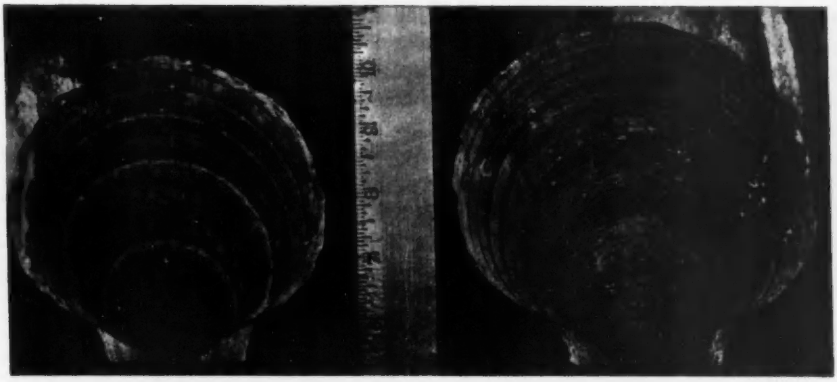

FIGURE 1. The left valves of two scallops from the Gulliver Cove area of the Bay of Fundy, showing some clear annual growth rings. The valve to the left was taken from an 8-year-old and that to the right from a 14-year-old scallop.

individual specimens. However, with the giant scallop which lives in deep water (10 to 50 fathoms) it is difficult to hold large numbers for sufficiently long periods to follow their growth. It is therefore necessary to rely on the less direct evidence from regular sampling of a given population. This paper reports observations on changes in the frequency distribution of rings on the valves of samples of scallops taken at intervals throughout a one and one-half year period, on the seasonal relationship between the position of the rings and the forming margin of the shell, and some observations on caged individuals. The results show that the growth rings are annual rings formed during the winter months when water temperatures are at a minimum for the year. The position and appearance of the first annulus have also been determined and with this information it has been possible to establish a general growth curve for scallops from part of the Digby area of the Bay of Fundy.

CHANGES IN RING FREQUENCY WITH SEASON

Samples of scallops were obtained from a bed 3½ miles northwest of Gulliver Cove in the Digby area of the Bay of Fundy at approximately monthly intervals from February 20, 1935, to August 6, 1936, inclusive, and the number of growth rings on the left (upper) valve of each scallop was determined. The left valve was used because the ring markings on it are more prominent and are less confused by incidental check marks or by chipping of the shell than are those on the right valve on which the scallop normally lies.

The percentage ring-frequency distribution for each of the samples is shown in Figure 2. In February, 1935, 45 per cent of the sample was composed of scallops bearing 6 rings, 20 per cent had 7 rings, 11 per cent had 4 rings, and the remaining 24 per cent was distributed among shells bearing 3, 5, or from 8 to 11 rings. The March sample was essentially the same. In April, however, the

6-ring group was reduced in favour of the 7, and this shift continued until June when the sample was composed primarily of scallops with 7 rings. The 4-group which had shown up in February was replaced in May by a prominent 5-group, and this continued, with the 7-group, to characterize the samples taken throughout the remainder of 1935.

During the early part of 1936 changes again occurred in the ring-frequency distribution. By February the formerly prominent 7-group was reduced and by May was almost completely replaced by the 8-group. During the same period a

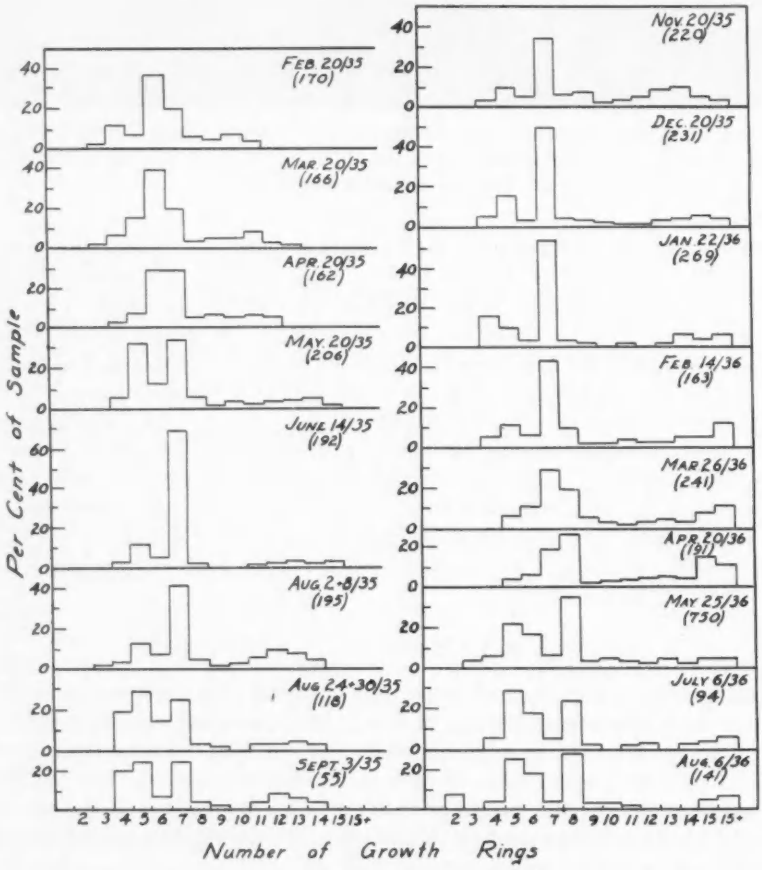

FIGURE 2. Percentage frequency distribution of growth rings on scallops taken from the Gulliver Cove bed in the Digby area at intervals from February 20, 1935, to August 6, 1936, inclusive. The May and August, 1936, samples were taken with a commercial drag lined with fine netting to retain small scallops. The remainder are samples taken by commercial gear having a 2⅝-inch inside mesh diameter. (The number of scallops in each sample is shown in brackets under date of collection.)

prominent 6-group seems to have replaced the former 5-group and a new, stronger 5-group appeared in the samples.

It may be inferred from this series that the groups bearing different numbers of rings represent certain year-classes of scallops which vary in strength. The shifting of the modal ring-groups during the period February to May in both 1935 and 1936 indicates that new rings are formed on the shells during the winter growing season. The absence of any shift during August and September, when scallops spawn, shows that it is not a spawning ring such as has been found in *Pecten irradians*. The growth rings appear, therefore, to be annual rings formed only during the winter. This conclusion is supported by further observations.

SEASONAL RELATION OF THE RING TO THE FORMING MARGIN

The five samples collected from February 20 through June 14, 1935, were examined and classified according to whether a growth ring was absent, was in

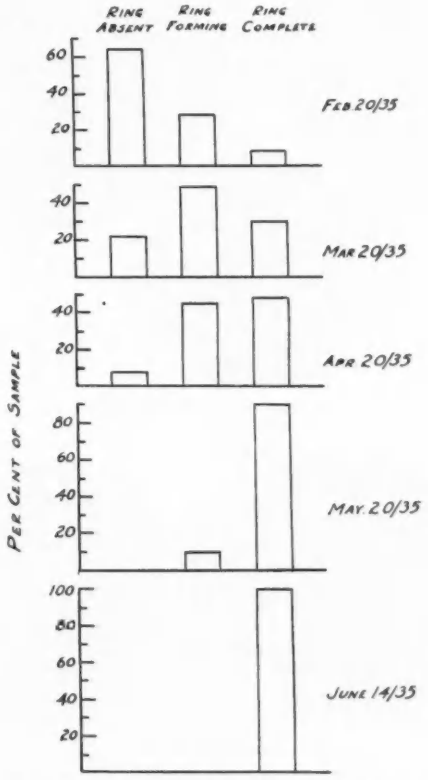

FIGURE 3. Percentage of shells from the Gulliver Cove bed having no ring, ring forming, or ring completed on the growing margin, indicating that new rings are formed during the late winter months.

the process of formation, or was complete, at the edge of the shell. The results of this classification are given in Figure 3. On February 20, 8 per cent of them had complete new rings, but 64 per cent lacked them. By March 20, 30 per cent had completed them and only 22 per cent lacked them. All scallops in the June 14 sample had completed the new growth ring.

These results confirm the evidence, from the shifting of the modes of the percentage ring-frequency distribution, that during the winter months from February to May a new ring is deposited at the margin of the shell. Since scallops ranging in shell height from 70 to 150 mm., bearing from 3 to 15 rings (Fig. 2), were included in this classification, it appears that all rings formed on the shell may be considered as annual rings.

FIGURE 4. Five of the scallops dredged from L'Etang River on August 30, 1934, nicked with a file and left to grow for 9¾ months, showing the sharp check mark formed at the position of the nick, and the band of added shell bearing a winter growth ring.

TABLE I. The growth of scallops obtained from L'Etang River, N.B., on August 30, 1934, nicked with a file to mark the edge of the shell, and submerged for 9½ months.

Scallop No.	Initial shell height	Total growth while in box	Growth: Nick mark to new ring	Final shell height
		Dead at end of experiment		
	mm.	*mm.*	*mm.*	*mm.*
1	79.5	3.3	3.3	82.8
2	84.0	2.0	2.0	86.0
3	86.0	1.9	..	87.9
4	86.5	no growth	..	86.5
5	87.5	nick repaired	..	87.5
6	90.0	1.0	..	91.0
7	92.0	no growth	..	92.0
8	99.5	nick repaired	..	99.5
9	112.0	nick repaired	..	112.0
10	115.0	nick repaired	..	115.0
11	115.0	nick repaired	..	115.0
12	115.0	3.7	..	118.7
13	118.0	1.5	..	119.5
14	119.0	no growth	..	119.0
15	122.0	no growth	..	122.0
16	123.0	no growth	..	123.0
17	129.0	3.0	..	132.0
18	133.0	nick repaired	..	133.0
19	135.0	nick repaired	..	135.0
		Living at end of experiment		
1	65.9	13.8	10.2	79.7
2	79.4	6.3	4.3	85.7
3	80.0	10.6	5.4	90.6
4	83.6	10.7	5.0	94.3
5	84.3	6.7	4.7	91.0
6	84.9	10.2	6.5	95.1
7	95.5	4.8	3.0	100.3
8	101.4	6.8	4.7	108.2
9	104.0	5.9	3.4	109.9
10	106.1	3.8	2.0	109.9
11	107.0	5.7	3.7	112.7
12	108.5	5.4	3.4	113.9
13	121.0	3.0	2.0	124.0
14	123.2	nick repaired	..	123.2
15	125.9	3.5	2.5	129.4
16	130.0	2.6	2.1	132.6
17	130.8	3.3	2.4	134.1
18	140.9	3.7	2.4	144.6
Average (living only)		6.3	4.0	

Ratio of: $\frac{\text{growth to ring}}{\text{total growth during experiment}} = \frac{4.0}{6.3 = 63.5\%}$

OBSERVATIONS ON CAGED SCALLOPS

On August 30, 1934, 37 scallops of different sizes were dredged from a bed near the mouth of L'Etang River in Passamaquoddy Bay. The height of the left valve of each was recorded and the margin nicked with a file. They were then placed in a large box, the ends of which were constructed of wire to permit the free passage of water, and the box was anchored on the bottom in Passamaquoddy Bay near the Atlantic Biological Station.

On June 14, 1935, the box was hauled and the scallops re-examined. Nineteen of them had died, but Table I shows that most of both the living and the dead had apparently grown during their period of submergence. All of the 37, except 5 of the dead animals, had deposited new shell in or beyond the nick mark. In every case where growth took place beyond the nick, a sharp check mark separated the old and new shell, and presumably reflected the sudden interruption of growth resulting from the shock of dredging and handling (Fig. 4). The new shell resembled that previously deposited except that in the case of dark shells it was lighter in colour. A growth ring had been formed at the margin of the shell of the two smallest dead scallops, and on all but one of the living.

The growth of the surviving scallops indicates the time of the deposition of the ring. One very large one did not appear to have grown at all during the experiment, but each of the remaining 17 had added a band of new shell and deposited a growth ring about two-thirds (63.5 per cent) of the way from the shock mark to the edge. Since the coldest water of the year occurred in February and March, or when about two-thirds of the period of submergence had passed, it appears that the new rings must have been deposited during the cold-water period. These results, therefore, confirm the conclusion that the growth ring is an annual ring deposited during the winter.

THE FIRST GROWTH RING

In early studies of the growth rings on shells ranging in height from 50 to 150 mm., the first growth ring, which is often difficult to detect, was missed. Old scallops may have the umbonal region of the shell so badly worn or eroded that the striae are nearly obliterated. Furthermore, during the early life of scallops there seems to be little seasonal variation in the rate of growth; the striae deposited during the first winters are closer together than those deposited during the summers, but are not crowded, so that the winter growth zone is poorly defined, and the early rings are less distinct than those formed later. However, the appearance of the first ring and the height of the valves at the time of its formation have been established from three collections of small scallops. The first collection was made in the Bay of Fundy during 1950 by the junior author, and the other two were made in Penobscot Bay during 1951 by Mr. F. T. Baird of the Maine Department of Sea and Shore Fisheries, Fisheries Research Laboratory, Boothbay Harbour, Me. (Baird, 1953). Mr. Baird generously made a number of his specimens available for study and comparison with the Bay of Fundy collections.

The Bay of Fundy collection, made in September, 1950, consisted of 53 small scallops ranging from 8 to 30 mm. in shell height. Since spawning in this area does not take place until late autumn, it was concluded that they must have passed at least one winter growth period and belonged to the 1949 or an earlier year-class.

The first Penobscot Bay collection was made in March, 1951, which established that they had passed at least their first winter. Mr. Baird placed them in an aquarium, and when the writer examined 24 of them in September, 1951, they ranged in height from 7 to 15 mm. Their size confirmed the conclusion that even the smallest of the Digby collection had passed at least their first winter.

The size of the Penobscot Bay shells at the time of deposition of the first annulus could be determined from a distinct check mark present at from 1 to 4 mm. from the umbo. This mark was in the form of a thin, narrow band of shell overlying the main surface, and is interpreted by the writer as representing the edge of the shell at the time the collection was made in March. It appears that when the animals were collected the mantle edge, which secretes the outer layer of the shell (Drew, 1906), was withdrawn, and when growth was resumed in the tanks new shell was added from a point behind the former edge. Since the growth ring is in process of formation during March, this shock mark indicates its position. Close spacing of striae at about this point on both the Penobscot Bay and Digby shells may, therefore, be considered to represent their first growth ring.

That this ring is the first rather than the second is confirmed by Baird's December 1951 collection, consisting of small scallop larvae found clinging to bryozoan growth. Their shells varied in height from 0.75 to about 2.0 mm. and none of them showed signs of close spacing of the striae such as denotes winter growth. The findings of Drew (1906) and Stevenson (1936) that scallop veliger larvae average about 1.0 mm. previous to settling, combined with the information from these collections of small scallops, therefore, limits the height of scallops at the time of formation of the first annual growth ring from about 1 to 15 mm., and indicates that the ring found within these limits on the shells is the first.

Examination of shells from a variety of year-classes from Digby indicates that in this area scallops are from 1 to 10 mm., and average about 6.7 mm., in shell height at the time the first ring is deposited.

THE GROWTH RATE OF DIGBY SCALLOPS

The demonstration that the growth rings formed by crowding of striae on the valves of the giant scallop are annual rings, and the establishment of the position and appearance of the first annulus, permits the study of the growth rate of populations of this species.

Measurements of 2,738 annuli were made on 437 shells collected from three beds off Digby during the summer of 1950 and a summary is presented in Table II. Size was measured as the straight-line distance from the umbo to each annulus, along the diameter passing through the umbo, and is, therefore, equivalent to the

TABLE II. Average size of inshore Digby scallops of different year-classes at time of formation of the annuli—1950 shell collections.

Year-class	Average shell height at formation of annulus No.												No. in year-class
	1	2	3	4	5	6	7	8	9	10	11	12	
Sample #1, Shelburne Cove, 2nd Ridge, July 24/50													
1947	8.0	19.0	40.0							2			4
1946	6.5	14.5	24.4	69.7									13
1945	8.3	17.4	30.1	54.4	82.4								9
1944	6.8	15.2	28.6	55.6	76.6	94.2							5
1943	7.0	15.0	28.5	61.8	81.3	94.3	105.0						4
1942	7.2	14.7	25.9	54.9	78.8	93.7	104.1	111.3					31
1941	7.1	14.7	25.4	53.8	78.9	93.9	103.5	109.9	113.7				37
1940	6.8	14.3	25.1	50.0	74.6	90.8	101.7	108.1	112.5	115.1			9
1938	6.7	15.0	24.3	53.3	78.0	92.0	102.0	109.7	116.3	122.0	123.0	125.0	3
1937	6.0	13.0	21.5	53.0	78.0	92.5	107.0	114.5	122.0	128.0	131.5	133.5	2
1936	6.0	11.0	17.0	47.0	75.0	89.0	101.0	110.0	117.0	124.0	128.0	132.0	1
Average	7.1	15.0	26.7	55.9	78.7	92.6	103.6	110.3	114.0	118.8	126.7	129.0	
Sample #2, Buoy Ground, Aug. 3/50													
1946	5.2	11.8	21.3	36.5									22
1945	6.4	14.6	25.6	46.5	68.1								10
1944	6.9	14.3	24.9	40.5	62.7	85.5							20
1942	5.0	10.5	18.5	31.0	60.5	82.0	98.5	108.5					2
1941	5.5	10.9	17.6	31.0	56.5	84.3	100.8	110.9	118.0				13
1940	5.4	11.3	18.3	30.1	54.7	81.4	100.1	110.6	117.6	121.8			18
1939	5.3	10.3	18.2	29.3	54.2	79.2	96.0	106.7	114.7	119.8	124.3		6
1937	5.5	10.5	19.3	32.8	60.3	86.0	102.5	113.5	120.0	126.3	131.3	135.0	4
1935	5.3	11.0	19.2	33.6	58.2	82.6	99.4	111.0	118.6	125.4	131.2	134.4	5
1934	5.1	11.0	17.1	28.3	52.0	77.0	95.7	107.3	115.1	122.6	127.2	131.3	14
Average	5.7	12.1	20.5	34.7	58.3	82.0	98.9	109.7	117.1	122.6	127.9	132.6	

TABLE II (*Cont'd*).

Year-class	Average shell height at formation of Annulus No.												No. in year-class
	1	2	3	4	5	6	7	8	9	10	11	12	
	Sample #3, Buoy Ground, Aug. 4/50												
1947	6.3	15.6	27.6										7
1946	6.7	15.6	27.2	40.7									135
1945	7.9	19.1	33.6	52.4	72.8								48
1944	7.4	17.8	33.6	55.0	77.6	96.4							5
1943	6.0	17.5	31.5	52.0	75.5	96.0	108.0						2
1942	8.7	17.0	29.1	55.6	80.0	93.0	103.3	114.3					3
1941	7.0	15.3	29.3	57.0	78.5	94.0	104.0	113.0	119.0				4
1940	6.0	11.0	19.0	34.0	61.0	90.0	104.0	113.0	120.0	122.0			1
Average	7.0	16.5	28.9	44.5	73.8	94.6	104.6	113.5	119.2	122.0			
Number of measurements	437	437	437	426	256	189	159	153	117	63	35	29	2,738
Average—all samples	6.7	14.9	26.1	45.0	70.2	88.1	101.8	110.2	115.8	121.6	127.7	131.9	
Standard deviation	1.0	2.7	5.8	11.6	10.0	5.8	3.2	2.4	2.6	3.4	3.2	3.3	

total shell height of the scallop at the time each annulus was formed. From these data a growth curve for each sample and an average curve for the three samples has been calculated and is shown in Figure 5.

The growth curve shows a typical sigmoid pattern with growth rate increasing up to an inflection point which is reached at about four years of age, or at about 55 mm. shell height. Thereafter growth rate decreases, and tends toward the upper asymptote, between 150 and 160 mm. However, there is considerable variation in size attained by each year-class at each age. The amount of variation has been measured as the standard deviation of the mean size at formation of the annulus of each year-class about the general mean size at that annulus, and has been marked on the growth curve. Also shown on the figure is the range in average size of each year-class at the time of formation of each annulus.

The amount of variation in size of scallops at any age appears to be small at first but increases rapidly during the first four years when the animals are growing rapidly. Thereafter the amount of variation decreases as scallops more

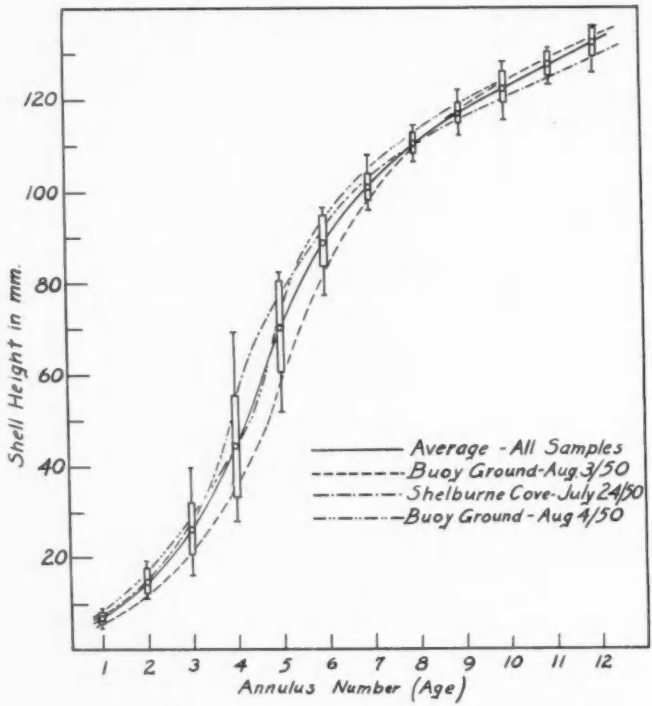

FIGURE 5. The growth of Digby scallops from three inshore areas. Vertical boxes represent ± 1 standard deviation and the vertical lines the range in average size attained by the year-classes included in the samples.

fully realize the growth potential for the species under growing conditions prevailing in the Bay of Fundy. The range in average year-class size, defined by one standard deviation above and below the general mean, does not overlap from one age-group to another until scallops are about eight years of age or about 110 mm. in diameter. This indicates that in studies of scallop populations year-classes may be reliably identified from modes in size-frequency distributions up to about the 110-mm. size.

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